ANNALS

OF THE

NEW YORK ACADEMY OF SCIENCES

VOLUME XXXVII

NEW YORK
PUBLISHED BY THE ACADEMY
1937–1938

Editor

JOHN HENDLEY BARNHART

Assistant Editors

ERICH MAREN SCHLAIKJER

(Pages 163-256)

RICHARD PINKHAM HALL

(Pages 257-328)

CONTENTS OF VOLUME XXXVII

DATES OF PUBLICATION AND EDITIONS OF THE BROCHURES

	Edition
Pp. 1–96, 29 October, 1937	1525 copies
Pp. 97–162, 18 April, 1938	1650 copies
Pp. 163–256, 11 May, 1938	1600 copies
Pp. 257–272, 10 June, 1938	1900 copies
Pp. 273–328, 5 July, 1938	1900 copies

Annals of the New York Academy of Sciences
Volume XXXVII, pages 1–96
October, 1937

OSTEOLOGY, MYOLOGY, AND PROBABLE EVOLUTION OF THE NEMATOGNATH PELVIC GIRDLE*

By Frederick Fey Shelden

CONTENTS

* Awarded an A. Cressy Morrison Prize in Natural Science in 1936 by the New York Academy of Sciences. Publication made possible through a grant from the income of the Centennial Fund.

INTRODUCTION

Outline of Treatment

Twelve species of nematognaths, representing eight families, were investigated in detail, and the pelvic osteology of three more forms was examined. The pelvic region was dissected, and rough drawings were made at each stage of the dissection. These drawings were later finished off and reproduced, and are presented in the paper.

A review of the literature upon the pelvic region of catfish and upon related subjects is included. This covers taxonomy, myology, osteology, functions, and evolution of the pelvic fins.

Then follows a discussion of the osteology of the pelves studied; this is purely anatomical in character.

Next the anatomy of the musculature of this region is taken up. This is followed by a discussion of the mode of action of the pelvic muscles, and the variations of these muscles and their osteological substructures in forms which use their fins in peculiar ways.

The last portion of the paper treats the evolution of the nematognath pelvis within the group, or more properly, the relative complexity and possible relationships of the various forms are hypothesized. These relationships are depicted in the form of phylogenetic trees.

Acknowledgment

The author wishes to take this opportunity to express his gratitude to those who have made possible the production of this thesis:

To Dr. William King Gregory, curator of comparative anatomy at the American Museum of Natural History, upon whose suggestion the work was begun, and under whose guidance the major portion of it was carried out; to Professor Archie Wilmot Bray, head of the department of biology at Rensselaer Polytechnic Institute, whose assistance in the preparation of plates and in the solution of questionable points was indispensable; to Dr. Robert H. Luce, for helpful suggestions as to arrangement of manuscript, and for reading the historical review; to G. Miles Conrad of the American Museum of Natural History, whose interest and advice in the work were extremely valuable; to C. M. Breder, Jr. of the New York Aquarium at Battery Park, who was a constant source of materials and valuable criticism; to Miss Francesca LaMonte of the Department of Ichthyclogy at the

American Museum of Natural History, who was ever ready to help with the taxonomy and related phases of the work; to J. R. Norman, Esq., assistant keeper of the department of zoology, British Museum (Natural History), London, for drawings of the pelvic girdle of *Diplomystes* (FIGURES 27 and 28) and a specimen of *Belone trachura* from Pernambuco; to Mrs. Helen Ziska, one of the artists of the American Museum of Natural History, for the drawings of the osseous girdles of *Hexanematichthys*, *Ameiurus*, *Ageneiosus*, *Xenocara*, and *Corydoras* (FIGURES 18–20, 24 and 26); to Professor Homer Heath Nugent of the English department of Rensselaer Polytechnic Institute, for aid in the literary phase of the work; to Miss Maxine Whittemore, Miss Eugenie Coleman, Mrs. H. W. Carey, and Booth Carey, for their ceaseless efforts and encouragement in all phases of the work, and without whose assistance and support this work could not have been produced on time; and to Miss Harriet Peck, librarian of the Rensselaer Polytechnic Institute and to the library staff of the American Museum of Natural History, who by their consideration and cooperation made the work on the literature a pleasure.

The Problem and Its Scope

This paper is the result of two and a half months' work at the American Museum of Natural History under the direction of Dr. William K. Gregory during the summer of 1935, and the continuation of this work during the scholastic year 1935–36 in the biology department at the Rensselaer Polytechnic Institute under the direction of Professor Archie W. Bray.

This investigation involves the solution of three problems: (1) What are the morphological characteristics of the bones and muscles in the pelvic region of the nematognath fishes? (2) What is the most probable evolution of the pelvis within this group? (3) Can the variety of uses to which these fishes put their pelvic fins be explained upon the basis of anatomical variations?

In order to deal with these problems, certain information is necessary. In the first place, a knowledge of just what the nematognath fishes are is prerequisite. In order to discuss intelligibly the first question, a knowledge of the general terminology and topography of the pelvic region is necessary. For the complete analysis of the second problem, it is essential that the general evolution of the pelvis from its very beginnings be understood. It would be almost impossible to answer the last question without having a knowledge of the customary

mode of usage and action of the paired and unpaired fins of fishes in general.

Although the general evolution of the pelvis has been worked out by many authors and some have treated the problem of evolution within the teleost group in a cursory manner, no one has, to the author's knowledge, attempted to explain the phylogenetic development of the pelvis in a limited division of the teleosts. It is the stated purpose of this paper, to attempt an explanation of the evolution of the various pelvic structures within the sub-order Nematognathi.

The study of the osteology and myology is undertaken for two reasons: first, in order to explain upon a morphological basis the numerous peculiar functions to which various members of this group may put their pelvic fins; and second, in order to have a frame of reference upon which to postulate the evolution of the pelvis.

It is hoped that this discussion may lead to a more detailed investigation into the relationship between the members of the teleost group. This might possibly lead to some explanation of the relation of the pelvic organization of Pisces to that of the tetrapods. It is also believed that the pelvic girdle of fishes, if more fully investigated, may be of some value in identification of fossil forms or of diagnostic value in placing some of the modern forms in their proper places taxonomically.

HISTORICAL REVIEW OF THE LITERATURE

Taxonomy

The nematognaths, or catfishes, are malacopterygian fishes of the order *Ostariophysi* (Boulenger, 1904; Regan, 1911; Jordan, 1905 and 1923; Nichols, 1930). According to most authors they are the most highly specialized of all the *Ostariophysi*. The only group that has any claim to greater specialization is that of the gymnotids, or electric eels; it, however, is a small group of about ten species, all limited to South America. Furthermore, they are probably derived from an ancestor intermediate between the nematognaths and the lower groups of the order, characins and cyprinids (Macfarlane, 1923).

The nematognaths agree with all other *Ostariophysi* in the absence of basisphenoid and opisthotic, and the presence of a well-developed Weberian apparatus. This latter has apparently been derived from portions of the first four vertebrae in all *Ostariophysi* and the fifth vertebra, as well, in the nematognaths (Regan, 1911), since these

bones are bound together into a complex which forms and supports the apparatus. The Weberian apparatus serves to connect the inner ear to the external medium *via* the air-bladder, the connecting link being the Weberian ossicles, according to Bridge and Haddon (1893). Gregory (1933) points out that this highly complex organization could hardly have arisen by convergent evolution, and that its presence, consequently, must signify that all of the *Ostariophysi* are derived from a common ancestor. This view is supported by Macfarlane (1923), who bases his views primarily upon paleontological evidence. The fact that the group, *Ostariophysi*, is derived from a single ancestral type is important in making valid any evolutionary comparison within the group.

The nematognaths are distinguished from the rest of the order by general skeletal characteristics such as the extreme atrophy of the toothless maxillary in all but *Diplomystes*, the most primitive species (Regan, 1911), peculiarities of the skull, pointed out by both Gregory and Regan, such as constant presence of the operculum and interoperculum, and various external characteristics used by all workers in the field. Examples of these external characteristics are: total absence of scales in all forms but *Lepidoglanis*, according to Jordan (1923), the body being either naked or covered with bony plates of various types, which are discussed completely by Leege (1922); and the presence of characteristic barbels, especially the maxillary barbel, which has the degenerate maxillary as its base. Still another identification mark is the presence of a spine on the anterior border of dorsal and pectoral fins, formed by the fusion of the first two rays.

The order *Nematognathi* was first established by Dr. Gill in 1870 and was further delineated by Cope as follows:

> "Precoracoid arch present. No coronoid or symplectic bones. Parietals and suproccipital confluent; four anterior vertebrae co-ossified, and with ossicula auditus. No mesopterygium. Basis cranii and pterotic bone simple; third superior pharyngeal bone wanting, or small and resting on the fourth; second directed backward. One or two pairs of basal branchihyals, two pairs of branchihyals. Suboperculum wanting, premaxillary forming mouth-border above. Interclavicles present."

Since, in *Diplomystes*, the maxillary is toothed and forms the mouth-border above, a change in this characterization is necessary. *Diplomystes* was raised to the rank of a family by Eigenmann & Eigenmann in 1888. The number of families into which the nematognaths are divided varies considerably. Cuvier & Valenciennes and Günther

united all the forms into a single family, *Siluridae.* Agassiz insisted that the differences between some of the genera was of sufficient magnitude to warrant family distinction. This summary of the history of the classification of nematognaths has been taken from Eigenmann & Eigenmann (1890).

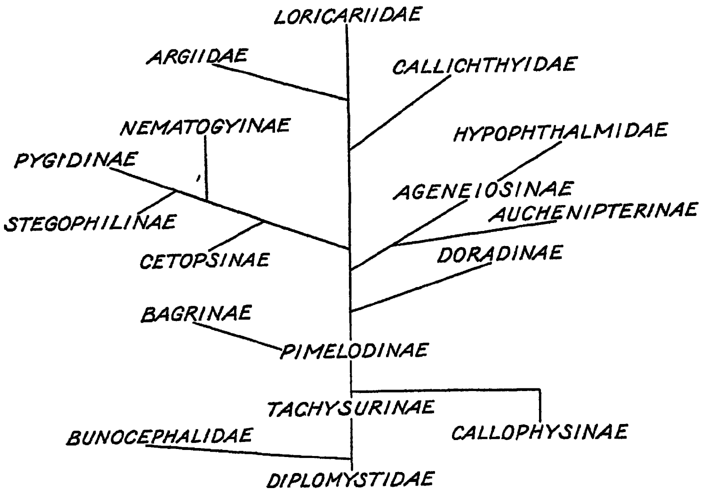
Jordan (1923) divides the nematognaths into twenty-seven families, while Regan (1911) has only twenty-three. The following is Regan's list arranged in order of increasing specialization and complexity, as interpreted by him:

1. Diplomystidae
2. Ariidae
3. Doradidae
4. Plotosidae
5. Siluridae
6. Bagridae
7. Ameiuridae
8. Amblycipitidae
9. Sisoridae
10. Amphiliidae
11. Chacidae
12. Schilbeidae
13. Clariidae
14. Pangasiidae
15. Synodontidae
16. Malapteruridae
17. Pimelodidae
18. Helogenidae
19. Hypophthalmidae
20. Trichomycteridae
21. Bunocephalidae
22. Callichthyidae
23. Loricariidae

The first family stands alone because of its generally simplified form. The next two families (2 and 3) have generalized external characteristics but an aberrant form of pectoral girdle. Families 4 and 5 are primitive in many ways, but have a highly developed anal fin. The *Bagridae* (6) are slightly more specialized generally than the preceding forms. *Ameiuridae* may be regarded as the American representatives of this group, and families 8 to 15 are designated as specialized bagrids. Families 16 to 21 are to be regarded as a loosely bound group slightly more developed than the bagrids with two exceptions, the *Malapteruridae* (16), or electric catfish, and the aberrant bunocephalids (21). *Callichthyidae* (22) and *Loricariidae* (23) are highly specialized forms. Of the latter, the *Loricariinae* are armored forms, and the *Arginae* are their unarmored relatives. "Silurids" is a general term used to designate all of the families except the *Loricariidae.*

The distinction between the various families is made upon the basis of skeletal variations, number and character of barbels, position of the eyes, number of rays in the pelvic fins, distribution of teeth, character of the union of the gills across the isthmus, presence or absence of armor, and other general characters.

Eigenmann & Eigenmann's analysis of South American forms and their relationships is depicted in the phylogenetic DIAGRAM A:



A

Functional Idiosyncrasies

Breder in 1935 issued a paper in which he raised the question of the presence of morphological variations in the pelvic myology to account for a wide variety of uses to which the members of this group put their pelvic fins. In this paper there is advanced a rough phylogenetic series based upon the reproductive habits of the various forms. He also discusses a number of peculiar functions to which the pelvic fins are put in reproductive and other activities. It seems appropriate to consider this paper in some detail.

Breder (1935) carefully noted the reproductive habits of *Ameiurus nebulosus* (Le Soeur) in an aquarium tank. When the pair are ready to spawn they seek a sheltered spot, often beside a submerged log or stone, and dig a shallow pit in the gravel of the bottom of the tank by pushing with their snouts, vigorous fanning of the pectoral fins, and powerful lateral swipes of the caudal region of the body. Some authors, Smith (1903) for instance, have observed the fish removing gravel in their mouths. When the "nest" has been completed, the pair, after some preliminary courtship play, lie side by side facing in opposite directions, and the spawning takes place. The eggs are numerous and coherent, forming a large jelly-like mass. One of the parents, usually

the female, starts to incubate the eggs immediately after they are laid and it is this incubating activity that is of interest in the development of the present author's theme. The incubating position is directly on top of the egg-mass and the activity is mainly an extremely vigorous beating up and down of the pelvic fins, although side swipes of the caudal region are also used. Occasionally clumps of eggs are taken into the mouth, chewing motions performed, and the eggs are then spit out. This is no doubt helpful in the aeration of the eggs. *Opladelus olivaris* (Rafinesque) and *Ictalurus punctatus* (Rafinesque), the mud catfish and the channel cat respectively, are reported as having similar habits.

Hexanematichthys australis (Günther) lives in rapid streams, and makes an excavation in which to lay the eggs, but, unlike *Ameiurus*, covers them with gravel after they are laid. It is evident that this form is easily derived from the primitive type of *Ameiurus*, and that this habit would tend to persist in the struggle for survival in that particular environment, since it would prevent the eggs from being washed away by the rapid current. The mode of derivation from the ameiurid habit is connected with the oral manipulation of the egg-mass or with the fanning activities. In the first case the pebbles would be taken into the mouth along with the eggs, while in the second, the fanning activities would lead to the filling of the nest excavation with pebbles.

The only set of reproductive reflexes which is more simple is found in the case of *Schilbeodes*, in which Fowler (1917) reports, according to Breder, that the eggs are laid, and the parents merely lie beside them, there being no attempt at incubation or nest-building. This is extremely primitive, of course.

Felichthys and *Arius*, where the species have been observed to reproduce, as well as *Conorynchus nelsoni* (Evermann & Goldsborough), which Breder is inclined to place among the ariids, are all oral-incubators. That is to say, they carry the eggs in their mouths while these are developing. These forms are all marine, and the majority of them apparently breed in estuarine waters where the bottom is soft rather than hard and gravelly. This breeding habit, therefore, is one that gets rid of the difficulty of the eggs sinking in the mud and smothering by sinking into it, as most nematognath eggs need high oxygen tension and continuous aeration, with the exception of some few South American forms which are rather far removed from *Ameiurus* and the marine cats. It is also possible to derive this habit from the ameiurid type because of the habit, noted in the latter, of taking the eggs into their

mouths Another factor that would help this type of reproductive habit to become dominant in the struggle for existence in this environment, is the fact that there are many more animals that would eat the eggs living on the bottom of the marine waters than there are in fresh waters, and oral incubation counteracts this source of danger.

Aspredo and *Bunocephalus* carry the eggs attached to the ventral surface of the body. This is, of course, a protective measure, for it enables the parents to carry the eggs with them when they flee from danger. It is easily derived from the ameiurid habit of lying on the eggs and is accompanied by a change in abdominal integument.

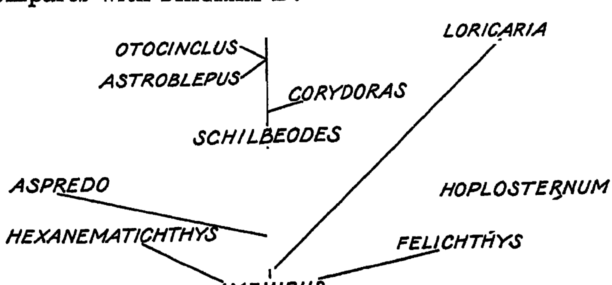
Loricaria vetula (C. & V.) and some of the other loricariids carry the eggs tucked in under the highly developed ventral labial fold. This is a protective act for the same reason as was mentioned in connection with *Aspredo,* and is likewise easily derived from the habit of lying on the eggs, since the flap would be a natural trap for the eggs.

Hoplosternum and *Callichthys* breed their eggs upon the under side of a floating raft of plant debris (Carter & Beadle, 1931). These nests are always found in poorly aerated waters, and there are many bubbles beneath them. This is a beneficial habit in that it gets the eggs nearer the surface, and therefore, in water of higher oxygen tension. Since the eggs apparently do not float by themselves, some sort of a mechanism is necessary to get them up under the raft. Carter & Beadle report that the eggs are stuck to the raft by a secretion; they do not state whether or not the secretion is oral, but it seems probable that it is. If this is the case, then this habit is derivable from the oral manipulation in *Ameiurus;* however, the exact method of derivation is not clear. One advantage of the bubbles is that they surround the eggs with water of increased oxygen tension.

Otocinclus, Corydoras, Astroblepus, and *Silurus* all have similar reproductive habits, the main element of which is casting free adhesive eggs. There are minor variations, but the most interesting habit of all is that of *Corydoras,* wherein the female forms a funnel-like basket of the pelvic fins in which eggs are held several at a time, to be fertilized (Carbonnier, 1881; Innes, 1935). They are then attached to plants. The other forms merely lay adhesive eggs on plants, where they are fertilized. The habit of *Corydoras* might bring about a better proportion of fertilization, and it might possibly be derived from the ameiurid habits of lying on the eggs and incubating them with the pelvic fins. The basic act of laying eggs that are adhesive to plants has some advantages for the survival of the eggs. In the first place, it keeps the eggs away from the bottom, out of reach of enemies that

might lurk there, and also prevents the eggs from sinking in soft mud. Second, it places the eggs in a region of higher oxygen tension, during the daytime, at least, since plants produce oxygen under the influence of sunlight. The derivation of this habit is a problem that does not have a superficial solution. Although it appears to be a rather primitive type of activity, Breder thinks that it represents a form that has passed through the ameiurid stage. This is a logical assumption, when the facts of the case are considered, for most of these forms are highly developed; they have complex uses for their pelvic fins, which may have been derived from ameiurid incubating activity. Furthermore, the eggs are not laid haphazardly on the bottom, the most primitive method. With regard to the special functions mentioned in the preceding statement, the habit which *Corydoras* has of forming a basket of the pelvic fins, has already been mentioned *Astroblepus* (*Arges*) is the genus of the so-called "walking catfish," and will be discussed below under the study of the functions of fins. *Otocinclus* grasps the stalk of a plant between the spines of its pelvic fins, and holds itself off the bottom in a vertical position by this means for considerable lengths of time. It is conceivable that the actions of *Otocinclus* and *Corydoras* are derivatives of the pelvic egg-fanning of *Ameiurus*.

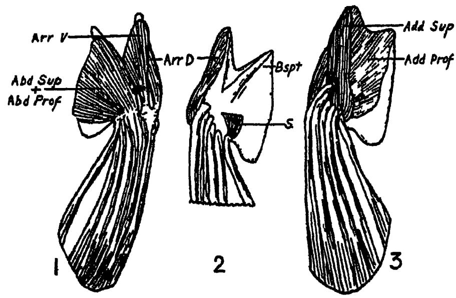
Breder points out the fact that the great gaps in the knowledge of the habits of many of the forms will not permit the formation of a hard and fast phylogenetic series upon the basis of reproductive habits. However, he believes that there are certain trends in the development of the various types which are quite clear. I have taken the liberty of showing this in the following diagram. I have also taken the privilege of inserting some of my own interpretations in the above discussion, which I believe follow from Breder's dissertation. It will be interesting to see how the phylogeny, based on the anatomy of the pelvis, compares with DIAGRAM B:



B

Myology

The myology of the pelvic region of teleost fishes has been thoroughly investigated as a general topic by Grenholm (1923). In his discussion of the pelvic myology of the nematognaths, he deals most completely with *Auchenoglanis occidentalis* (Cuvier & Val.) among the siluroids, and treats only muscles that are purely pelvic, that is, those which originate on the pelvic bones and insert on the fin-rays (see FIGURES 1, 2, 3). He separates these muscles into three sets of two muscles each. The three sets are the arrectors, the adductors, and the abductors. The arrector set is composed of an arrector dorsalis which originates on the lateral corner of the pelvis and inserts on the outer corner of the first ray, and the arrector ventralis (FIGURE 1, *Arr. V.*) which originates on the cranio-lateral process of the pelvis and inserts on the ventral process of the first ray. The abductor muscles are more or less coalesced, with their fibers going in the same direction on the ventral surface of the pelvis, and insert on the heads of rays 1 to 6. This combined muscle lies on the ventral side of the pelvis. The adductor muscles lie on the dorsal surface of the pelvis, and consist of an adductor superficialis and profundus. The origins and insertions are the same as those of the abductors, but on the dorsal side of the pelvis. The two muscles are definitely separate and their fibres run in different directions.



FIGURES 1–3. *Auchenoglanis occidentalis.* Half of pelvic region. FIGURE 1. Ventral view. FIGURE 2. Ventral view, with some muscles removed. FIGURE 3. Dorsal view. (All after Grenholm.)

Bspt., basipterygium. *Abd. Sup.* + *Abd. Prof.*, combined abductor superficialis and abductor profundus; *S.*, special slip of latter. *Add. Prof.*, adductor profundus. *Add. Sup.*, adductor superficialis. *Arr. D.*, arrector dorsalis. *Arr. V.*, arrector ventralis.

Although Grenholm does not discuss the action of the various muscles in *Auchenoglanis*, he does discuss the functions of the analagous muscles in *Gadus*, the cod. They are as follows:

Abductor superficialis draws rays downward and forward.
Arrector ventralis draws border-ray ("Randstrahl") forward and downward and broadens the fin.
Abductor profundus—same as abductor superficialis.
Arrector dorsalis draws first ray forwards and upwards; spreads fin.
Adductor superficialis draws fin upwards and backwards; folds fin.
Adductor profundus—same as adductor superficialis.

Grenholm also describes the pelvic myology of several other nematognaths. He finds that in *Arius commersonii* (Lacép.) there are two adductors and two abductors, and an arrector ventralis, as well as an arrector dorsalis. *Synodontis nigritis* Cuvier & Val. has the same complement of pelvic muscles as the above form. In *Exostoma oschanini* Harz there are certain peculiarities of the fin-muscles adapting it to its natural habitat, torrential mountain streams. However, these variations are more pronounced in the pectoral fins. There are no detailed descriptions or drawings of this form. The pelvis has full complement of six muscles.

Grenholm's study also brings out the fact that the myology is quite constant in character throughout the *Ostariophysi*, and does not vary to any startling extent among all of the teleosts.

McMurrich (1884) specifically treats the myology of *Ameiurus catus* (*A. nebulosus*). His description of the pelvic myology agrees with that of Grenholm for the most part, but he does not recognize the arrector muscles. From my own investigations, I am inclined to think that they are present even in this form.

McMurrich's interpretation of the action of the pelvis muscles is as follows:

Abductor superficialis abducts (pulls downwards) the fin and separates the rays.
Abductor profundus assists in abduction but does not separate rays.
Adductor superficialis adducts (pulls upwards) the fin; outer fibers also separate the rays.
Adductor profundus aids the adductor superficialis and tends to approximate the rays.

McMurrich goes farther than Grenholm, and discusses two pairs of muscles which, while not purely pelvic in nature, insert on the pelvis. These are, first, a portion of the infracarinales, or ventral muscles which insert on the posterior end of the pelvis, and originate, in part, on the basis of the anal fin. This pair of muscles is called the retractor

ischii, a name originated by Owen. The second set of muscles is a part of the great ventral muscle and is called the protractor ischii. The above-described muscles will appear again in the discussion of the "walking catfish." FIGURE 4 is a drawing based upon descriptions of McMurrich and the drawings of Carlisle, used to show the various regions of the myotomes.

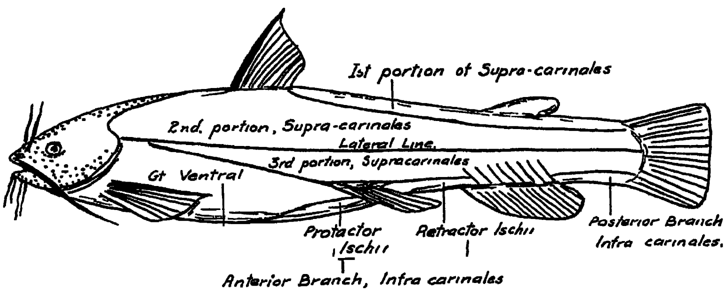


FIGURE 4. General regions of the myotomes (diagrammatic).

Evolution

The general evolution of the pelvis in the class Pisces has been worked out completely and more than once on anatomic, embryologic, and paleontologic bases. That is to say, the transformation from the primitive cartilaginous pelvis of the shark, and from even further back among the oldest forms, through the *Holostei* and *Chondrostei*, up to the generalized teleost form, has been hypothesized. However, no one, to the author's knowledge, has dealt very completely with the evolution in the teleost group, and still less within such a definite group as the nematognaths.

Sewertzoff (1934) gives one of the most complete and up to date discussions of this problem. Although it is not the purpose of the present paper to deal with the general evolution of the pelvis through all the groups of fishes, it seems wise to give a brief review of this evolution in order to understand better the anatomy of the region, and also what is happening in the evolution within the small group studied by the present author.

The view adopted by both Sewertzoff (1934) and Goodrich (1930), as well as by numerous other investigators in this field, is that put forth by Balfour and Thacher, according to Goodrich. The first step in the development of the paired fins is the formation of a pair of ventrolateral fin-folds running a goodly portion of the length of the body.

The endoskeleton of the paired fins arose in this fold and at its base, as segmentally arranged separate skeletal centers in the form of short rods. However, this view does not coincide with that of Gegenbaur, which is that the limb-girdles and their appendages have been derived by the posterior migration of gill-arches and gill-flaps. Nevertheless, the end result would be the same in both cases. According to the view of Goodrich, the primitive type of girdle arose by concresence and concentration of the rod-like skeletal elements. The result is a girdle of the type found in the Devonian cladoselachians, and very similar to the pelvic girdle of the modern *Ceratodus* (FIGURE 5). The compar-

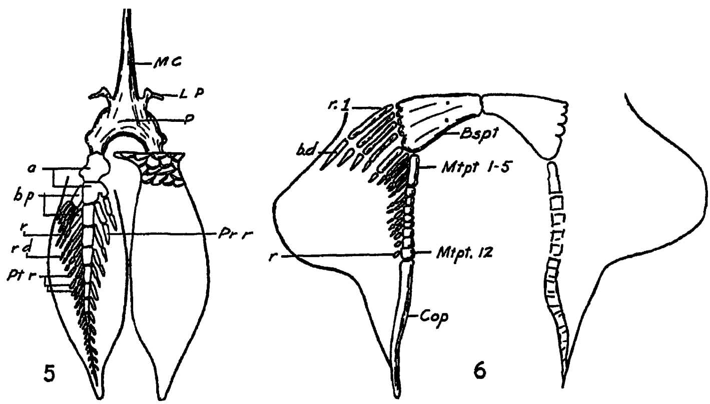


FIGURE 5. *Ceratodus*. Pelvic girdle. (After Grenholm.)
P., pelvic plate; *L. P.*, its lateral (prepubic) process. *M. C.*, median cartilage. *a.*, axis. *b. p.*, basalia proximalia. *r.*, radialia. *r. d.*, radialia distalia. *Pr. r.*, preaxial radials. *Pt. r.*, postaxial radials.

FIGURE 6. *Hybodus*. Pelvic girdle. (After Sewertzoff.)
Bspt., basipterygium. *Mtpt.*, metapterygium. *b. d.*, basalia distalia. *r.*, radialia. *Cop.*, copulare.

able evolution of the pectoral and pelvic fins is borne out by the work of Derjugin, Grieb & Trifonowa (1934), in which it is shown that the ontogenetic development of the two girdles is rather similar and that the more primitive character of the pelvic region is due mainly to a later start and structural modifications corresponding to functional variations. Briefly, the pelvis of *Ceratodus* consists of a median segmented axis in the fin which articulates with a pelvic girdle, cartilaginous in character, which is situated in the ventral abdominal wall. On the anterior and posterior side of this axis there are articulated radial elements composed of from one to three segments each. The segments proximal to the axis are designated as basalia proximalia (*b. p.*), those intermediate as radials, and those distal from the axis

as radialia distalia (*r. d.*). Those radial elements on the anterior side of the axis are the pre-axial radials (*Pr. r.*), and those on the posterior side are post-axial radials (*Pt. r.*). This whole organization is designated as the biserial archipterygium. Possibly this axis in the course of time rotated into the body, and the post-axial radials disappeared. Going back to an earlier stage in the development it is probable that there was independent concrescence, concentration, and inward extension of the rod-like elements postulated by Goodrich (1930) which occurred more rapidly in the anterior portion of the fin-rudiment. This process would have given rise to a pair of median basal elements to the outer side of which there articulated a number of radials, the remains of the original rod-like elements. These latter views are supported by the appearance of segmented "Anlagen" of the basal elements in the ontogenetic development of certain forms (*e. g.*, *Acipenser ruthenus*, FIGURE 8). We will discuss this form later. In the development of this type of pelvis the two sides often meet and fuse in the mid-line. These methods of origin mentioned above mean, as is pointed out by Sewertzoff (1934), that the base of the fin will be long, and parallel to the long axis of the body. There is a considerable gap between these early forms, as found in *Pleuracanthus*, and an arbitrarily chosen following stage which occurs in *Hybodus*, another fossil shark.

In *Hybodus* (FIGURE 6) it is seen that the anterior basalia have combined with the pelvic girdle, which shall be designated as the basipterygium. Some have also coalesced with the remains of the axis, and these segments are now known as the metapterygia. In the posterior part of the fin some of the basalia have combined with the radials. In *Scyllium*, the European dogfish, the pelvis shows slightly higher development. The general structure is the same as in *Hybodus*, but the metapterygium is unsegmented. In the modern ray, *Raja blanda*, there is found a very similar condition, but a dorsally directed rod-like process is present which is similar to the one shown in the pelvis of *Ceratodus*. Goodrich designates this process as the prepubic process.

A higher stage, or an off-shoot of the former, occurs in the *Chondrostei*, more specifically in *Huso huso* (FIGURE 7). Here is seen a condition similar to that occurring in *Scyllium*, but in addition there occurs a dorsally directed process of the basipterygium comparable to the prepubic process of Goodrich, but which Sewertzoff designates as an iliac process. The two basipterygia in this form do not unite across

the mid-line. It will be noted that in this case the number of segments in the metapterygium is reduced compared to the number in *Hybodus*, the number of radials is reduced, and more of them articulate with the basipterygium. These changes are all toward simplification. It might be well to emphasize the fact that all previously discussed pelvic structures have been cartilaginous.

It is of interest to note, as shown by Sewertzoff, that in the embryological development of *Acipenser ruthenus*, the segmented character of

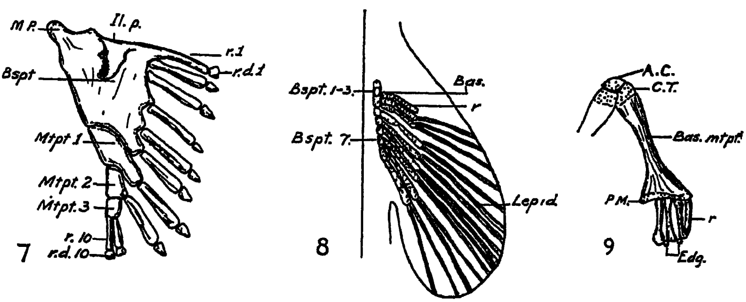


FIGURE 7. *Huso huso*. Pelvic girdle. (After Sewertzoff.)
Bspt., basipterygium. *Il. p.*, iliac process. *M. P.*, median process. *Mtpt.*, metapterygium. *r.*, radialia. *r. d.*, radialia distalia.

FIGURE 8. *Acipenser ruthenus* (immature). Pelvic girdle. (After Sewertzoff.)
Bspt., basipterygium. *Bas.*, basalia. *r.*, radialia. *Lepid.*, lepidotrichia.

FIGURE 9. *Polypterus birchir*. Pelvic girdle. (After Davidoff.)
A. C., anterior cartilage. *Bas. mtpt.*, basipterygium (mesapterygium basale of Davidoff); *C. T.*, its cartilaginous tip. *P. M.*, processus medialis. *r.*, radialia. *Edg.*, radialia distalia ("Endgliedestücke" of Davidoff).

the basipterygium, which has been hypothesized in the phylogenetic development, reappears in the ontogenetic development. Here is more evidence that the basipterygium is formed from a number of small basal elements. (See FIGURE 8.)

Another gap now occurs, and it is necessary to proceed from *Scyllium* and *Acipenser* to the *Crossopterygii* (*Polypterus birchir*) (see FIGURE 9). In *Polypterus* it is evident that the basipterygium (*Bas. mtpt.*) has changed considerably. It is longer, ossified, and has rotated so that the long axes of the basipterygia are no longer perpendicular to the long axis of the body, but form an acute angle with it. With this change there is also a change in the position of the fins. The base has become narrower, and is no longer parallel to the long axis of the body, but is more nearly perpendicular, and the lepidotrichia point caudally rather than laterally. This variation persists throughout all higher

forms. It is also of note, that the radials have greatly decreased in number, and the metapterygium is no longer segmented. According to Davidoff (1880), the bony rod-like part of the pelvis in this form is not the analogue of the basipterygium in the selachians. The latter is represented by the cartilaginous pieces (FIGURE 9, *A. C.*, *C. T.*) attached to the anterior end of the main pelvis. The bony rod (*Bas. mtpt.*), Davidoff believes, is derived from metapterygial elements in the selachian pelvis. The processus medialis (*P. M.*) is of interest, for this is the part of the girdle which forms a connection between the two halves of the pelvis in higher forms. It is worthy of note that the connection between the two halves of the pelvis in *Selachia* is at the anterior end of the girdle while the processus medialis is at the posterior end. Here, the separate metapterygial elements are all absent, the number of radials is still further reduced, and they are ossified.

Amia is of particular interest, for, as Macfarlane (1923), Gregory (1933), and others point out, this is similar to the form from which the teleost stem was probably derived. The *Holostei* (*Amia* and *Lepidosteus*) come higher in the evolutionary scale than *Polypterus*. The anterior cartilaginous pieces found in this latter form have become much reduced, and the radials are fewer, smaller, and not ossified. Although a piece designated by Sewertzoff (1934) as a metapterygium (FIGURE 10, *Mtpt.*) is slightly larger and is ossified, there is no apparent reason for considering anything of this type as being other than a radial. In this discussion, the bony rod (FIGURE 9, *Bas. mtpt.* and FIGURE 10, *Bspt.*) will be designated as the basipterygium, and the large medial piece articulated to it the metapterygium, although the probability is kept in mind that these may or may not be analogous to the structures of similar name found in *Selachia*.

The highest complexity is found in the teleosts. Sewertzoff states that the number of forms in this group is so great that it would be almost impossible to make a detailed study. He merely gives a number of forms to show the general trend in the development.

In *Salmo salar* (FIGURE 11), the position of fins and basipterygium is very similar to that found in *Holostei*, but in a medial direction there has developed a broad flat bony plate (*Bspt.* (*Pl.*)) attached along the rachis (*Bspt.* (*Rac.*)), which represents the basipterygium in the *Holostei*. Furthermore, the two basipterygia are united across the midline in their posterior region by means of a medially-directed cartilaginous process designated by Sewertzoff as the processus medialis of the basipterygium. In *Salmo*, the radials have become very

rudimentary, and so has the metapterygium. There is also another posterior outgrowth (*Proc. med. post.*) of the basipterygium. This is unossified, and is designated by Sewertzoff as the processus medialis posterior of the basipterygium. This is another part of the pelvis that will be of importance in the present author's thesis. It is further to be noted, that with the morphological change, that is, shrinking of the metapterygium, there occurs in these latter forms a functional variation in that the number of lepidotrichia, or rays, articulating with the metapterygium becomes reduced so that, in the adult of *Salmo,* there are none. In the larval stages, however, five of the lepidotrichia

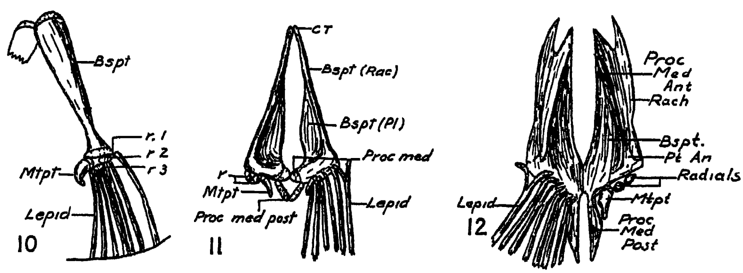


FIGURE 10. *Amia salva.* Pelvic girdle. (After Sewertzoff.)
Bspt., basipterygium. *Lepid.*, lepidotrichia. *Mtpt.*, metapterygium. *r.*, radialia.

FIGURE 11. *Salmo salar* Pelvic girdle. (After Sewertzoff.)
Bspt., basipterygium (*Rac.*, rachis, *Pl*, plate); *C. T.*, its cartilaginous tip. *Lepid.*, lepidotrichia. *Mtpt*, metapterygium. *Proc. med.*, processus medialis. *Proc. med. post.*, processus medialis posterior. *r.*, radialia.

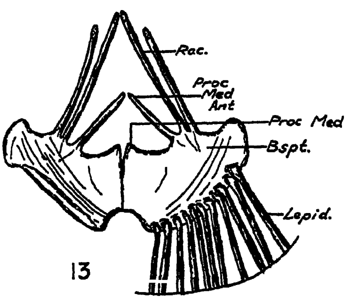
FIGURE 12. *Cyprinus carpio.* Pelvic girdle. (After Sewertzoff.)
Bspt, basipterygium. *Lepid.*, lepidotrichia. *Mtpt.*, metapterygium. *Proc. Med. Ant.*, processus medialis anterior. *Proc. Med. Post.*, processus medialis posterior. *Pt. An.*, processus analis. *Rach.*, rachis.

articulate with the metapterygium, again showing recapitulation of a primitive condition.

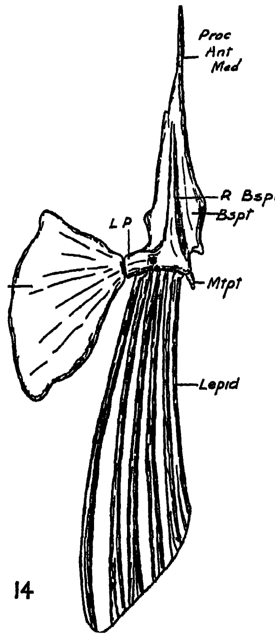
In the adult pelvis of the carp, *Cyprinus carpio* (FIGURE 12), we have a very similar condition except that the processus medialis posterior is larger and ossified, and the anterior end of the basipterygium is broader and bifurcated. The outer part (*Rach.*) represents the rachis appearing in *Salmo,* which is in turn a derivative of the rod-like basipterygium in *Polypterus* and *Amia;* the inner half (*Bspt.*) is an extension of the former comparable to the plate (*Bspt.* (*Pl.*)) in *Salmo.*

Sewertzoff gives only one nematognath pelvis. This is that of an immature *Silurus glanis.* In this form, the basipterygia are broadly

united across the mid-line by a large processus medialis (FIGURE 13, *Proc. Med.*). The metapterygium and the radials are absent. From the anterior end there extend three bony rod-like processes. The most lateral process (*Rac.*) represents the rachis of lower forms, the intermediate corresponds to the internal branch of the bifurcation in *Cyprinus*, and the most medial process is the analogue of the processus medialis anterior (*Proc. Med. Ant.*) of simpler forms.



13



14

FIGURE 13. *Silurus glanis* (immature). Pelvic girdle. (After Sewertzoff.)
Bspt., basipterygium. *Lepid.*, lepidotrichia. *Proc. Med.*, processus medialis. *Proc Med. Ant.*, processus medialis anterior. *Rac.*, rachis.

FIGURE 14. *Belone acus* (adult). Pelvic girdle. (After Sewertzoff.)
Bspt., basipterygium; *R. Bspt.*, its ridge. *B. L. P.*, bony lateral process articulated with basipterygium. *L. P.*, lateral process. *Lepid.*, lepidotrichia. *Mtpt.*, metapterygium. *Proc. Ant. Med.*, processus medialis anterior.

The only other form that will be taken up here is that of a synentognath, *Belone acus* (FIGURE 14), which is mentioned because Sewertzoff postulates an articulated lateral process (*B. L. P.*) in this form. In many ways, this is a more primitive form than *Silurus*, since there is a metapterygium, and the broadly united flat basipterygia of *Silurus* appear in *Belone* as a pair of rod-like unconnected bony processes.

The articulated lateral process of this form is of interest because there is apparently no other mention of such a process in the literature, and because such a process was discovered by the present author in the loricariids. Furthermore, from examination of closely related syn-entognaths, it appears that Sewertzoff has made a mistake, and this process is fused rather than articulated.

In this discussion of the internal elements of the pelvic fins, the origin and development of the fin-rays or lepidotrichia of teleosts has been neglected. Briefly, they may be considered as being derived from rhomboidal bony scales of the body. Both Goodrich and Sewertzoff have found intermediate stages between the typical scales of the body region and the bony segments of the lepidotrichia. These primitive rhomboidal scales have also given rise to cycloid and ctenoid scales of many types on the bodies of the various fishes. These scales vary widely between the groups. Now, although the scales and the lepido-trichia are apparently derived from the same source, the former vary greatly among the various groups of fishes while the form of the latter is relatively constant. Sewertzoff attributes this condition to two factors:

> (1) The lepidotrichia in the ancestors of the bony fishes had taken their characteristic form before the various fishes had been derived.
>
> (2) Once the lepidotrichia were formed they had a great similarity in function which tended to keep their form constant.

The derivation of the nematognath pelvis has been traced from its most primitive beginnings, and it is hoped that this discussion will aid in the understanding of the present author's thesis. A more detailed description of the derivation of the nematognath pelvis from the lower *Ostariophysi* will be undertaken in the discussion of the evolution within the former group.

Before leaving the osteology of the pelvis of the nematognaths, it might be well to consider for a moment McMurrich's (1884) analysis of the pelvis of *Ameiurus catus* (*A. nebulosus*). He describes the plate as consisting "of two similar pieces united in the middle line. The anterior part of each piece is very thin, and is produced into a point at the outer angle. The posterior edge is rounded, and gives articulating surfaces for the rays of the ventral fin—eight in number. Posteriorly in the mid-line there is a horse-shoe shaped cartilage, the concavity of which is directed backwards, the two limbs of which give attachment to portions of the infracarinales muscles [retractor ischii]."

Functions of Fins

Having discussed the osteology, myology, and evolution of the ventral fins of the fishes under consideration, it is logical to turn next to the uses of these pelvic fins. The first activity that fins bring to mind is that of locomotion. Dugès (1905), Breder (1926), Carlisle (1808), and Grenholm (1923) fairly agree that the fins of fishes in general, especially the paired fins, are unimportant as motor agents in locomotion, but act more as rudders and stabilizers. The most complete and modern discussion of locomotion and use of fins in fishes is given by Breder (1926). He divides the methods of locomotion into three primary types.

> (1) *Anguilliform.* Primarily, this type of locomotion consists in throwing the anterior part of the body into what is practically a sine curve, and passing this curve backwards by differential alternate serial contractions and relaxations of the myomeres.
>
> (2) *Ostraciiform.* This type of motion is characteristic of fishes whose bodies are enclosed in a test, and whose peduncle is too short to be thrown into waves. Side to side motion and paddling with the paired fins, primarily pectorals, are the main locomotor activities.
>
> (3) *Carangiform.* This type is intermediate between the two above forms. The fish do not throw their bodies into a series of reverse curves, as described for Anguilliform, nor are the bodies completely inflexible, as in the Ostraciiform, but the entire body flexes as from a fulcrum or pivot, the atlas.

The nematognath fishes illustrate a wide variety in modes of locomotion, ranging from almost ostraciiform in some of the *Plecostominae*, whose short body is completely covered with a thick armor, to almost anguilliform in some of the long narrow *Loricariidae* and plotosids.

In order to test the value of the various fins in locomotion, Breder experimentally disabled the fin or fins to be experimented with, either by cutting off the fin, or by freezing in liquid air. Osburn (1906), Grenholm (1923), and Carlisle (1806) performed similar experiments differing mainly in the method used for disabling fins. Breder found that, as a general rule, none of the fins was of very great importance as a propulsive organ, but that the main propulsive force was derived from an undulation of the body. If he made the body rigid by passing a wire through its length just above the vertebral column, little progress was made.

The paired fins, Breder believes, are used primarily in maneuvering, or more specifically, in turning, raising one or the other end of the body, stopping short, etc. It is true that the pectorals are the most

important in this activity, but the pelvics also play their part. The fins act in stopping the body by extension ventro-laterally with their flat surfaces perpendicular to the long axis of the body so that they provide a considerable resistance to forward motion; a unilateral extension would tend to turn the body to one side. As Breder points out, however, in a long fish, if the pectorals are extended, the resistance will tend to "trip up" the fish, that is, the anterior end will be forced down. This is where the pelvic fins come into play, for by extending them simultaneously with the pectorals, the tendency of the anterior end to sink is counteracted. Osburn (1906) noted that the pectoral fins, and in many forms the pelvics as well, were kept moving continously while the fish was suspended motionlessly in the water. He attributed this activity to an attempt on the part of the fish to keep itself in an upright position. Breder, on the contrary, believes that this waving of the paired fins serves merely to counteract the propulsive force of water spurted out of the gills during respiration. That is to say, if the paired fins were not in motion, the body would be driven forward by the force of the water expelled from the gill-chamber. Grenholm (1923) found upon amputation, that the loss of one fin is compensated for, in function, by the action of one of the remaining fins. Carlisle (1806) reports greater effects upon the fishes' equilibrium and locomotion when the various fins are amputated than do either of the preceding authors. When he removed all fins, paired and unpaired, the fish was almost without motion and floated upside down. When the tail was removed, neither the pelvic nor the pectoral fins were used to aid forward motion.

Although the fish may customarily compensate for the effect of the loss of any fin or fins, this does not mean that the fins have no function in the normal animal. The fins are moved often and vigorously at times, and therefore must have some function.

Probably the most peculiar activity to which the catfishes put their fins is that of walking on land, and climbing perpendicular and even overhanging walls. Various authors describe walking activities for a considerable number of catfishes. Leege (1922) states that *Plecostomus* and *Callichthys* can travel over land to new bodies of water when their old ones dry up. In these forms, he states, the main locomotor organs are the pectoral and ventral tail-spines. Schomburgk (1848) refers to the use of pelvic fins in overland travel, but Leege, after investigating the former author's sources of information, believes that this is a printer's error. Bridge & Haddon (1893) substantiate the

fact that *Callichthys* is capable of making progress out of water. The *Doradidae*, as walking cats, are discussed by Hancock (1828), who states that their main terrestrial locomotor organs are the heavy spines of the pectoral fins, and their pectoral muscles. This form, is, therefore, of little interest in this report. Another group of walking catfishes is composed of members of the sub-family *Arginae*. This group, according to Evermann & Kendall (1905) and Johnson (1912), use their pelvic fins in combination with the highly developed suctorial mouth as a means of locomotion. Johnson points out that *Arges marmoratus*, which he observed climbing vertical and even overhanging walls, is a poor swimmer, and usually creeps along the bottom of streams, rather than swims. It is really rather simple for this type of activity to be transferred from the bottom of a body of water to dry land. The protractor and retractor ischii in this form are highly specialized as comparatively long, cord-like muscles, and are capable of moving the pelvis a considerable distance in a longitudinal direction, one sixth of the body length, according to Johnson, and one half to three quarters of an inch in a fish whose length is not given, according to Evermann & Kendall. The latter authors claim that *Cyclopium* (probably synonymous with *Astroblepus* and *Arges*) can stay out of water for considerable periods of time without any apparent ill effect. They have observed two methods of locomotion on land used by this fish. In one type, the anterior end of the body is attached to the subsurface, which in this case must be smooth, and the posterior portion of the body is brought anteriorally by arching the body after the manner of an "inch-worm." The mouth is then released and the body shoved forward by extension of the myotomes, the spine on the bottom of the tail preventing backward slip. The second method is used on rough surfaces. Breder (1926) was unable to observe this second type of locomotion, and claims that locomotion is accomplished by a side to side flopping accompanied by synchronized activity on the part of the mouth, which is attached when the caudal extremity is bent laterally forward, and released when the body is straightened. It is evident that this motive progression can be used only upon such a surface that the suctorial attachment of the mouth is possible. The difference of opinion between Breder and Evermann & Kendall may be due to the fact that they were studying different forms.

Hora (1922–'23–'27), in discoursing on the changes that take place in the anatomy of the fauna of torrential streams, includes information upon various nematognaths, noting some significant changes in

the pelves of these forms. *Glyptosternon* and *Glyptothorax* present a condition in which the border-ray of the paired fins has become modified, and soft, pointed, cartilaginous rays are given off along the anterior margin. This modification is accompanied by a flattening of the bottom of the fish and a consequent broadening and depression of the body with a pushing of the roots of the fins from a ventral to a lateral position. These are all modifications which enable the organism to keep its body pressed closely against the subsurface, and thus prevent the torrent from sweeping it away. Regarding the myology of the pelvis, Hora (1922) states, "the pelvic fins also possess a special muscle beside the abductor and adductor systems. This keeps the fins closely

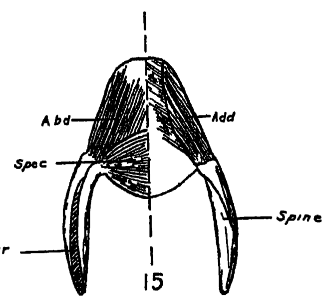


FIGURE 15. *Glyptothorax.* Pelvis; right half, dorsal view; left half, ventral view. (After Hora.)

Abd., abductor. *Add.*, adductor. *Spec.*, special muscle discussed by Hora. *Str.*, striations of first ray of pelvic fin.

pressed against rocks, when the fish is resting, thus enabling it to adhere to rocks by means of striated skin on the under surface of some of the outer rays of the pelvic fin." FIGURE 15 is a drawing taken from Hora's work to illustrate this modification. The drawing is not definite enough to enable one to determine the homolgies of this special muscle. In fact, as far as the drawing is concerned, the special muscle could very easily be a modified abductor superficialis. In *Pseudecheneis*, the ventrals possess long, curved bases, and there is an indication of a membranous fold between the two, anteriorly. This may be the beginning of a sucking disc-like pelvic fin-complex similar to that found in *Gastromyzon*, the Bornean sucker, a homalopterid.

It has been impossible to gain access to Koltzoff's work (1896) on the skeleton of the pelvic fins and Rautenfeld's inaugural dissertation (1882) upon the pelvic fin of ganoids and teleosts.

MATERIALS AND METHODS

The forms studied in detail are:

AMEIURIDAE.	*Ameiurus nebulosus* (Le Sueur)
ARIIDAE.	*Hexanematichthys* (*Galeichthys*) *felis* (Linn.)
DORADIDAE.	
Doradinae.	*Doras hancocki* (Cuvier & Valenciennes)
Ageneiosinae.	*Ageneiosus marmoratus* (Eigenmann)
PIMELODIDAE.	*Rhamdia* sp.
PLOTOSIDAE.	*Plotosus arab* Forskål
LORICARIIDAE.	
Loricariinae.	*Pterygoplichthys anisitoi* (Eigenmann & Kennedy)
	Xenocara chagresi (Eigenmann & Eigenmann)
	Farlowella amazonum (Günther)
Arginae.	*Astroblepus* (*Cyclopium*) *homodon* (Regan)
	Astroblepus longifilis (Steindachner)
CALLICHTHYIDAE.	*Corydoras paleatus* (Jenyns)
	Corydoras nattererii (Steindachner)

The families are taken from Regan's classification, the subfamily *Ageneiosinae* from Eigenmann & Eigenmann's phylogenetic tree.

The os pterygia of *Plecostomus, Loricaria, Felichthys,* and other genera were studied superficially, and the pelvis of *Diplomystes papillosus* was studied from drawings made by J. R. Norman.

The animals were all preserved, and the preservative was not the same in all cases. The state of preservation varied, some forms, one in particular, being almost hopelessly decomposed. The specimens were dissected carefully, using a dissecting microscope where necessary, and rough drawings were made at each stage of the dissection; the finished drawings were prepared later. The functions of the various pelvic-fin muscles were determined experimentally by exerting traction on them "in situ" parallel to the direction of their fibers, and observing the effect, or consequent motion of the fin-rays.

These conventions were used in the drawings:

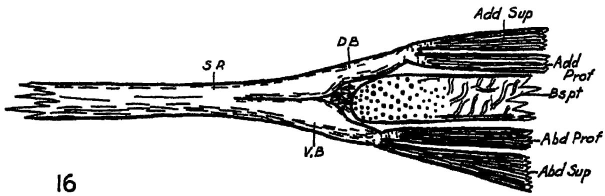
Stipple—cartilage
Continuous lines—muscle
Broken lines—tendon
Unshaded—bone

OSTEOLOGY

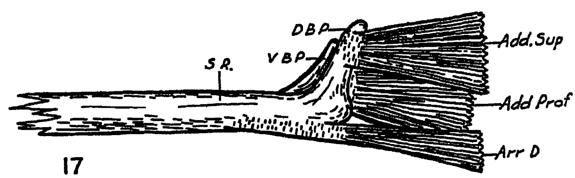
The Lepidotrichia

The lepidotrichia, or fin-rays, are the supporting elements for the fin proper. They are rod-like in structure, ossified, and bifurcated at their proximal end, which articulates with the basipterygium, and cornified or horny, segmented, and branched at their distal end (FIGURE 16). The edge of the basipterygium fits in between the dorsal and ventral branch of the bifurcated part of the ray, and the ray is kept in juxtaposition with the basipterygium by the tension of the muscles of the pelvis which insert on the fin-rays and originate on the basipterygium and also by a connective tissue which loosely joins the head of the ray and edge of the basipterygium. Both dorsal and ventral branch of the proximal end of the ray are expanded into a process, the head (FIGURE 16), which is at an angle of almost 90 degrees, in a horizontal plane, with the long axis in a vertical plane. The process on the dorsal side, is thicker at its base and tapers to a blunt point while the process on the ventral side is more blunt. When muscles insert on the distal end of the processes, a lever system of the first class is formed in a plane parallel with the basipterygium. The fulcrum is the point of articulation of the ray with the pelvis, the point of application of the force is the point of insertion of the muscle on the distal end of the head-process, and the resistance is provided by the friction of the fin as it passes through the water. The contraction of a muscle inserted at this point will cause the ray to rotate posteriorly. If, on the other hand, the muscle is inserted along the long axis of the fin we have a lever in a plane perpendicular to the basipterygium. The only element of the physical system that is changed is the point of application of the force. The contraction of a muscle so inserted will cause the ray to move dorsally or ventrally, depending upon which side the muscle is inserted, *i. e.*, whether it is dorsal or ventral. This is an extremely simplified view of the function of these muscles. The ossified part of the ray immediately distal to the head is known as the shank, and a pair of muscles—the arrector muscles, insert antero-laterally upon this portion of the ray. When we consider the action of these latter muscles we have a lever of the third class with the fulcrum at the point of articulation, the force or energy applied at the insertion of the muscle, and the resistance in the usual place. Contraction of these muscles will rotate the first ray pulling it anteriorly when the two act simultaneously and with no

complication from the other pelvic muscles when the first ray is drawn forward; any slack in the membrane between the rays is thus taken up and consequently the fin is spread fanwise. The superficialis muscles act in the manner first described, since they insert superficially on the distal end of the head-processes of the rays. The effect upon the fin is therefore abduction or adduction with simultaneous folding of the fin. The profundus muscles lie next to the basipterygium, have a deep insertion on the head of the rays, primarily in the region of the long



16



17

FIGURES 16 and 17. Head of a generalized first ray, showing details of insertion of muscles (diagrammatic). FIGURE 16, lateral view. FIGURE 17, top view.

Abd Prof., abductor profundus. *Abd. Sup.*, abductor superficialis. *Add. Prof.*, adductor profundus. *Add. Sup.*, adductor superficialis. *Arr. D.*, arrector dorsalis. *Bspt.*, basipterygium. *D. B.*, dorsal branch of bifurcation of ray; *D. B. P.*, its head process. *V. B.*, ventral branch of bifurcation of ray; *V. B. P.*, its head process. *S. R.*, shank of ray.

axis of the ray, and contraction will cause the second type of rotation discussed above. Contraction of these muscles, therefore, cause adduction or abduction of the fin without spreading or folding it. The diagrammatic representation of the structure of the rays and the insertion of the various muscles will be found in FIGURES 16 and 17.

In summarizing, therefore, it may be stated that the arrector muscles spread the fin, the profundus muscles adduct or abduct the fin without spreading or folding it. That is to say, the fin is rotated from its base dorsally or ventrally without any change in the extent of the fin-surface fixed by the action of the superficialis or adductor muscles. The superficialis muscles, on the contrary, either adduct or abduct, and simultaneously fold the fin, the folding being more pronounced when the contraction is in the dorsal muscle.

Ameiurus nebulosus

In *Ameiurus nebulosus* (FIGURE 18), which is arbitrarily chosen as the starting point in the discussion of the pelvic osteology, the basipterygium (*Bspt.*) consists of a broad flat plate. The two basipterygia are united across the mid-line forming a bilaterally symmetrical unit, the basal plate. From the anterior end of this basal plate there extend in an antero-medial direction two pairs of rod-like processes. These are the anterior processes, the more medial of which is designated as the internal process of the basipterygium (*I. P.*), while the more lateral processes are designated as the external processes of the basipterygium (*E. P.*). The anterior tips of the internal processes are united across the mid-line by a tendon-like connective tissue. The external processes extend more in an anterior direction than in a medial direction, and their tips do not approach each other. A membrane is stretched between these anterior processes, and serves as the point of origin for some parts of the pelvic musculature. The internal and external processes in *Ameiurus* are well ossified, especially in the region where the bases of the anterior processes extend on to the plate as ridges of more densely osseous tissue. The plate proper is pierced by several neural foramina. The median connection between the two halves of the basal plate is cartilaginous and forms a strip of considerable width (*M. C.*). Therefore, we have a hinge-like structure, the basal plate being flexible along the mid-line. The pelvis is not perfectly flat, but is rather concave on the ventral side and convex on the dorsal side.

The posterio-lateral edge of the basipterygium is cartilaginous, and this is where the fin-rays, or the lepidotrichia, articulate.

From the posterior edge of the plate in the region of the median cartilage (*M. C.*) there extend a pair of posteriorly-directed, rod-like, cartilaginous processes, the posterior processes of the basipterygium (*P. P.*). The two processes are united at their base, and are tightly fused to the basal plate, and form what McMurrich (1893) calls a "horseshoe" shaped process. These processes serve as an insertion for a portion of the infracarinales, the retractor ischii (FIGURES 29 and 30, *R. I.*).

There are eight rays in the pelvic fin of this form.

Hexanematichthys (Galeichthys) felis

In this form (FIGURE 19), the basipterygium has the same general structure as in *Ameiurus*, but it is more heavily ossified. Each ex-

ternal anterior process bears a very pronounced ridge (*R. E. P.*). The anterior tips of the internal processes are not united across the mid-line, nor do they approach each other as closely as in *Ameiurus*, and the concavo-convex shape is more pronounced. There is no posterior process, the retractor ischii inserting directly upon the posterior end of the pelvis. As in *Ameiurus* there is a membrane stretched between the anterior processes. The innermost (most medial) ray, that is, the sixth ray of this form is highly modified. The bony structure is much heavier than that of the other rays, and it appears that it may have been derived by the fusion of two normal rays. Externally, this heavy bony structure is covered with a thick cartilaginous sheath which is heavier at the proximal end and this point is produced on the lateral side into a blunt knob somewhat curved in the form of a hook. This modified structure is designated as the clasper ray (*C. R.*). There are six rays in the pelvic fin.

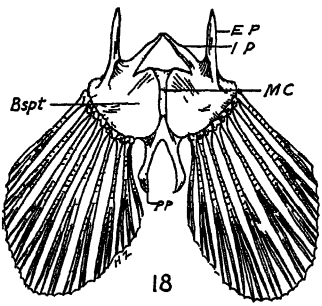
Doras hancocki

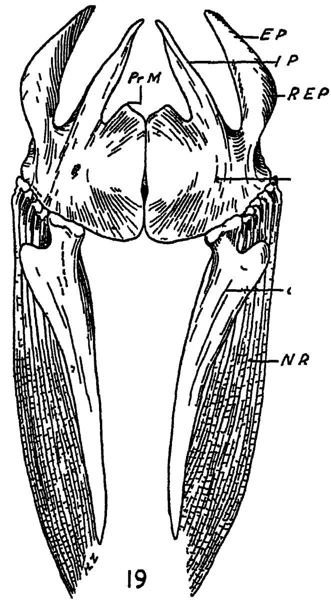
The dorsal part of the body is covered with a heavy armor, while the ventral is unarmored but covered by a thick tough skin. The pelvic girdle of *Doras* (FIGURE 36) is very similar to that of *Ameiurus*. The tips of the anterior processes (internal) are again united across the mid-line. The posterior processes are rod-like, cartilaginous, and more widely separated than in *Ameiurus*. There is one new feature, the so-called lateral process (*L. P.*). In *Doras* this is a cartilaginous extension of the basipterygium at the base of the external anterior process, and immediately anterior to the articulation of the first ray. The process extends antero-laterally in its proximal part, and then turns dorsal, finally inserting distally in the lateral body-wall muscles. It thus forms a loop about the tendon of the arrector dorsalis very similar to that found in *Plotosus*, and figured for this latter form (FIGURES 46 and 47). The possible function of this arrangement will be discussed later. It is worthy of a second mention, that this is the first form in which a lateral process is present. The pelvics are seven-rayed.

Ageneiosus marmoratus

Ageneiosus marmoratus is placed in the family *Doradidae* by Regan (1911), but Eigenmann & Eigenmann (1890) place it in a subfamily of the *Hypopthalmidae*, the *Ageneiosinae*, the family being taken off the phylogenetic stem later than the *Doradidae*. The pelvis (FIGURE 20) is somewhat similar to that of *Doras*, especially in the anterior

region. The main differences appear in the posterior and lateral processes. The latter (*L. P.*), although it is still cartilaginous, does not turn dorsally but extends laterally for its whole length. It does not insert on the general body-wall muscles as in the case of *Doras*, but has the superficial protractor lateralis inserted upon it in place of the two





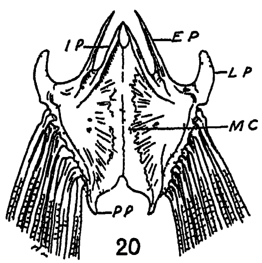


FIGURE 18 *Ameiurus nebulosus* Pelvic girdle, dorsal aspect.
Bspt, basipterygium *E P*, external anterior process *I P*, internal anterior process *M C*, median cartilage *P P*, posterior process

FIGURE 19 *Hexanematichthys (Galeichthys) felis* Pelvic girdle, dorsal aspect.
E P, external anterior process of basipterygium *R E P*, its ridge. *I P*, internal anterior process *Pr M*, processus medialis *N F*, neural foramen. *C. R.*, clasper ray *N R*, normal rays

FIGURE 20 *Ageneiosus marmoratus* Pelvic girdle, ventral aspect
E P, external anterior process of basipterygium *I P*, internal anterior process *L P*, lateral process *M C*, median cartilage *P. P*, posterior process

slips of this muscle which insert upon the lateral process of the former. Furthermore, the tendon of the arrector dorsalis has cut into the posterior edge of the process near its base and forms a notch at this point. The tips of the internal processes are united in the same manner as occurs in *Doras* and *Ameiurus*. The posterior process is cartilaginous, but in this form it is flat rather than rod-like, and passes insensibly into the body of the basipterygium. The concavo-convexity of the plate is less pronounced than in either of the previous

species. There is a broad cartilaginous area along the mid-line of the plate. In this form the pelvics are seven-rayed, and the first ray is unbifurcated and stouter than the other rays, although it is not stiffened to form a spine.

Rhamdia sp.

The *Rhamdia* specimen could not be specifically identified from external criteria, as it had been mutilated rather badly. The pelvics

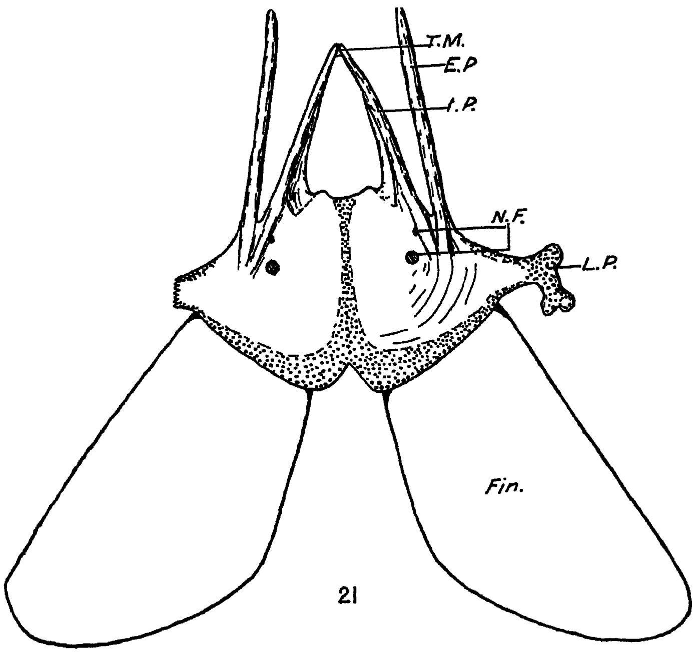


FIGURE 21. *Plotosus arab.* Pelvic girdle, dorsal aspect.
E. P., external anterior process of basipterygium. *I. P.*, internal anterior process. *L. P.*, lateral process. *N. F.*, neural foramina. *T. M.*, tendon medialis, connecting tips of internal anterior processes.

(FIGURE 40) are almost the exact counterpart of those of *Ameiurus*, except that there is a very small and rudimentary cartilaginous lateral process (*L. P.*). This process is flat, extends laterally for its whole length, and has a protractor lateralis (a slip of great ventral muscle) inserted on it. This is the simplest type of lateral process found in the author's investigation. The pelvic fins are six-rayed.

Plotosus arab

This (FIGURE 21) is another of the same general type as the preceding. The anterior tips of the internal processes are united as usual, the

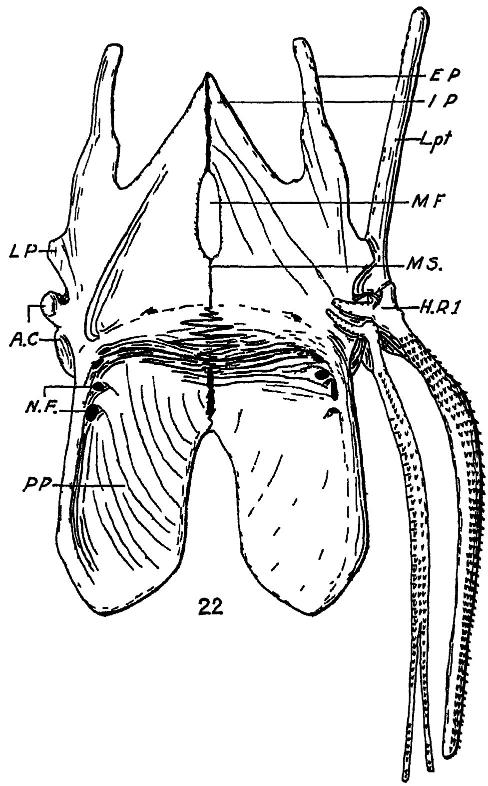
lateral process forms a loop around the tendon of the arrector dorsalis, as in *Doras*, and is cartilaginous. However, there is no posterior process, and, as in the case of *Hexanematichthys*, the retractor ischii inserts on the posterior end of the plate. The anterior processes are rod-like and relatively longer than in any of the former species. The major ossification of the plate occurs at the base of the anterior processes and in the central area of the basipterygium. The posterior and lateral border are cartilaginous as is the mid-line portion. The pelvics are eleven-rayed.

Pterygoplichthys anisitoi

The pelvis of *Pterygoplichthys* (FIGURES 22 and 23) is far removed from any of those discussed so far. This is one of the armored loricariids, and in correspondence with its general complexity the pelvis is highly specialized.

The basal plate is completely and heavily ossified, and the two halves are united in the posterior region by a serrated suture in the midline (*M. S.*). In the middle of the anterior end of the plate there occurs a foramen, the median foramen (*M. F.*). Anterior to this foramen the mid-line connection is formed by connective tissue. There is but a single pair of anterior processes (*E. P.*) which occupy the same position in relation to the other parts of the pelvis that the external processes occupy in lower forms. Medially the anterior end of the basal plate is produced in a triangular form, with the apex directed anteriorly; this area (*I. P.*) is homologous with the interior processes previously described. The foramen lies in the middle of this area and running parallel to the border of the triangular projection there are well developed pairs of ridges (*R. I. P.*); these ridges extend upon the surface of the plate. The anterior end of the triangular portion of the plate is inserted upon the ventral body-wall by means of a tendon. At the base of the external anterior process near the lateral edge of the plate, there are two articulating condyles (*A. C.*). The anterior one is ventro-lateral, the other is ventral. The former serves for the articulation of the first ray, the latter for the articulation of the other five. The external anterior process bears a very small bony lateral process (*L. P.*). At the base of the external process, and at a point just anterior to the first articulating condyle, there is a long, rod-like, well ossified bone which has been arbitrarily designated as lateropterygium (*Lpt.*). Approximately this structure articulates upon the anterior part of the first articulating condyle. The author has been unable to find any reference to a process articulating laterally with the

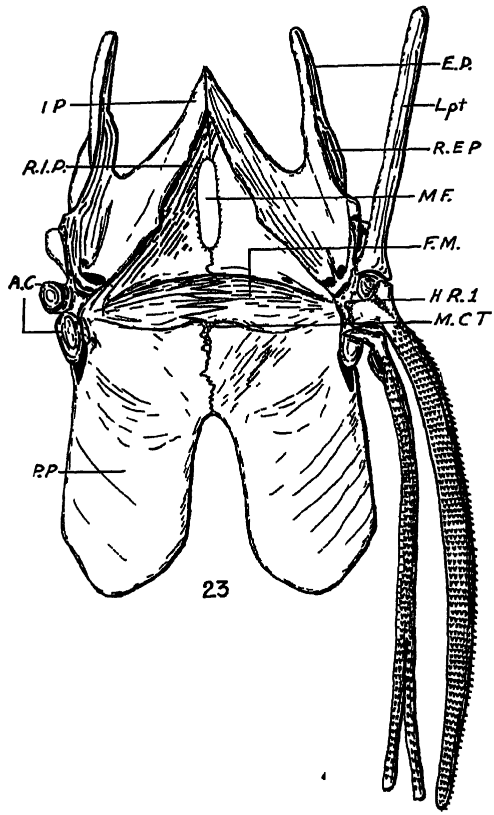
basipterygium, with the exception of such a structure referred to by Sewertzoff (1934) in *Belone acus* (FIGURE 14, *B. L. P.*). However, after dissection of several synentognaths, namely, *Tylosurus*, a close relative of *Belone*, according to Nichols & Breder (1928), *Parexocoetus*, and *Exonautes*, more highly specialized forms according to the above authors, and *Scomberesox*, an intermediate form, it was decided that



22

the lateral process in *Belone acus* was not articulated, but rather fused with the basipterygium, since in all the forms investigated the latter was the case. This hypothesis was further substantiated when it was found that the lateral process in *Belone trachura* was fused with the basipterygium. It would, therefore, appear that Sewertzoff was in error, and that the lateropterygium, as an articulated lateral process of the basipterygium, appears only in the *Loricariidae*. In *Pterygoplichthys* the lateropterygium is attached distally to the body armor by a tendon (FIGURE 48, *T. Lpt.*). The posterior processes (*P. P.*) are

an integral part of the basipterygium, there being no well defined limit between the two; they are broad, flat, heavily ossified plates. Upon the ventral surface of the plate there occurs a fossa, the fossa muscularis (*F. M.*) which takes the place of the ventral concavity of



FIGURES 22 and 23. *Pterygoplichthys anisitoi.* Pelvic girdle. FIGURE 22, dorsal view. FIGURE 23, ventral view.

E. P, external anterior process of basipterygium; *R. E. P.*, its ridge. *I. P.*, internal anterior process; *R. I. P.*, its ridge. *L. P.*, lateral process. *Lpt.*, lateropterygium. *M. F.*, median foramen. *M. S.*, median suture. *F. M.*, fossa muscularis (holds part of abductor profundus). *A. C.*, articulating condyles for rays. *H. R. 1*, head of first ray. *M. C. T.*, median cartilaginous tissue. *N. F.*, neural foramina. *P. P.*, posterior process.

the plate in the lower forms. In it there lie parts of the abductor profundus.

The first ray is very stout, unbifurcated, and stiffened to form a strong spine; the surface of this spine is covered with small, bony, posteriorally-pointed spinules. The pelvic fin is supported by six rays.

Xenocara chagresi

This is another of the armored loricariids. Its body is more depressed and broader than that of *Pterygoplichthys*, and correspondingly the basipterygium (FIGURE 24) is wider compared to its length than in the latter form. The pelvis is heavily ossified, and has a pronounced dorsal concavity. There is, however, a compensating fossa muscularis upon the ventral side, and this serves, as in *Pterygoplichthys*, for the insertion of parts of the profundus. The posterior processes are again ossified and integral parts of the basal plate. The lateropteryg-

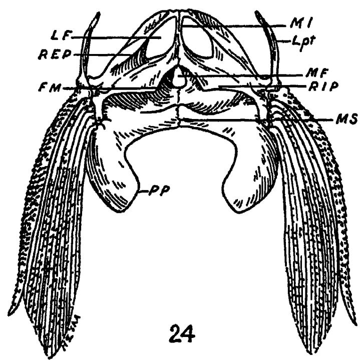


FIGURE 24. *Xenocara chagresi.* Pelvic girdle, ventral aspect
M. I., median bony isthmus. *Lpt.*, lateropterygium. *L. F.*, lateral foramen. *M. F.*, median foramen. *R. E. P.*, ridge of external process. *R. I. P*, ridge of internal process. *F. M.*, fossa muscularis. *M. S*, median suture. *P. P.*, posterior process.

ium is present, and in this case it is traversed by numerous small canals (FIGURE 52, *C. Lpt.*). There are no anterior processes. The anterior portion of the plate bears three foramina. One, the median foramen (*M. F.*) lies at the botton of the fossa muscularis, and is small and circular in shape. The other two lie more anteriorally, one on each side of an isthmus of bones lying in the mid-line (*M. I.*). These are designated as the lateral foramina (*L. F.*). The anterior end of the plate is attached to the ventral body-wall by means of a tendon, the anterior tendon (FIGURE 51, *A. T.*). Upon the ventral side of the anterior region of the basal plate, there occur two pairs of ridges. One pair runs almost transversely, and forms the anterior border of the fossa muscularis (FIGURE 24, *R.I.P.*). The second pair (*R. E. P.*) runs close to, and parallel with, the anterior edge of the plate. It thus lies between the anterior edge of the basal plate and the lateral foramina. The isthmus between the lateral foramina is formed of two halves joined along the mid-line by cartilaginous tissue. As in *Pterygoplich-*

thys, the posterior part of the plate is jointed in the mid-line by means of a serrated suture. Two articulating condyles are present. In *Xenocara*, the first ray is modified to form a rigid spine covered with small spinules just as in *Pterygoplichthys*. There are six rays in the pelvic fin.

Farlowella amazonum

Like the two species last described, this is one of the armored loricariids, and is the most completely armored form studied, the whole body being covered with hard bony scutes. The character of the basal plate (FIGURE 55) is very similar to that of *Pterygoplichthys*. The main differences are: first, the anterior processes are much shorter, and second, there is no lateropterygium. This latter condition may be due to faulty dissection of the single specimen available, since the presence of ventral armor and the small size of the pelvis made dissection difficult; however, this possibility is not likely. There is a single median foramen (*M. F.*), the posterior processes are flat and bony, and the ridges on the ventral surface of the plate are the same as in *Pterygoplichthys*. The anterior end of the plate is attached to the ventral body-armor by a tendon (FIGURE 56, *A. T.*). There are two articulating condyles.

Two other girdles, those of *Plecostomus* and *Loricaria*, were investigated superficially. They agree in all important details with *Pterygoplichthys*. As in other armored loricariids the pelvics are six-rayed. However, in this form the first ray, while heavy and covered with spinules, is not stiffened and is bifurcated, and, therefore, may not be considered a spine.

Astroblepus (Cyclopium) homodon

The girdle illustrated in FIGURE 25 is that of *Astroblepus longifilis*, while the drawings showing the myology are taken from the *Astroblepus homodon* specimen. The former was taken for the study of the osteology because it was larger; the two forms, however, are the same in both osteology and myology. The basal plate is flat, and not as heavy as that of the armored loricariids, although it is completely ossified. This girdle is depicted as viewed from the dorsal aspect. As in the case of *Pterygoplichthys*, there is but a single pair of anterior processes (*E. P.*); these are well ossified and rod-like, and they bend medially to a greater extent than do the same structures in the above species. The anterior end of the plate (*I. P.*) is triangular with a very acute apex. There are no foramina in the plate with the exception of neural foramina (*N. F.*). There is a slight ridge upon the dorsal side

of the plate which extends into this triangular region. At the base of the external process, there is a well developed, bony, lateral process (*L. P.*) upon which the protractor ischii inserts. The lateropterygium, in this form, is very thin, and has the shape of a battledore. The

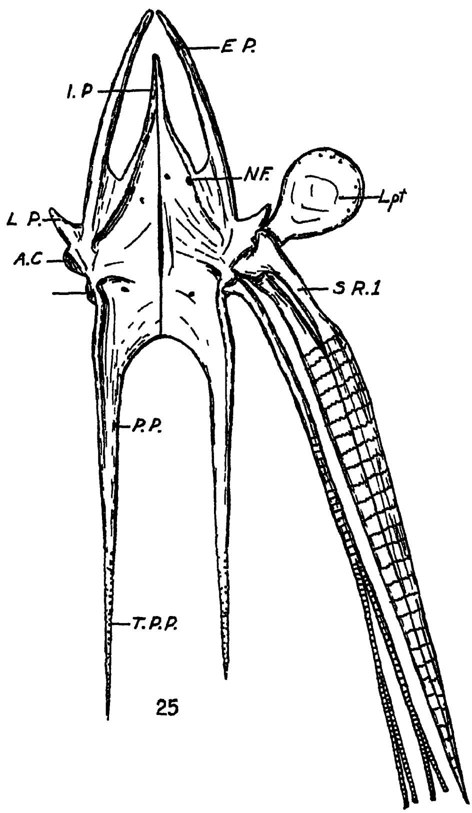


FIGURE 25. *Astroblepus longifilis.* Pelvic girdle, dorsal aspect.
E. P., external anterior process of basipterygium. *I. P.*, internal anterior process. *L. P.*, lateral process. *Lpt.*, lateropterygium. *N. F.*, neural foramen. *A. C.*, articulating condyles. *S. R. 1*, shank of first ray. *P. P.*, posterior process; *T. P. P.*, its cartilaginous tip.

"handle" part is attached by a tendon to the lateral edge of the basipterygium just posterior to the lateral process. The periphery of the lateropterygium is cartilaginous, the remainder ossified. There are no muscles inserted upon this structure, and it lies just beneath the skin, superficial to the body-wall muscles, and anchored only by the subcutaneous fascia. There are two articulating condyles (*A. C.*),

which have the same function as those of the armored loricariids. Posterior processes are ossified, rod-like, and are an integral part of the basipterygium. Their distal tips are cartilaginous and thread-like.

In this form the border-ray is again developed to form a spine, although the latter is not as stout as those of the armored loricariids. There are five rays in the pelvic fins.

Corydoras paleatus

The specimen of the above species investigated in this study was a female. In order to determine whether there was any sexual dimor-

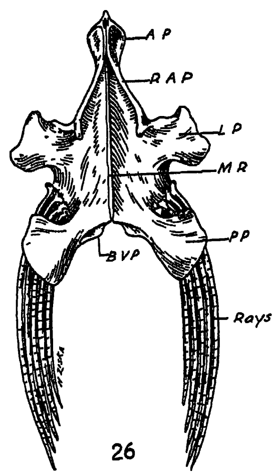
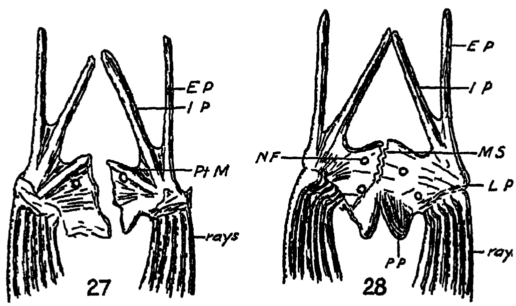


FIGURE 26. *Corydoras paleatus.* Pelvic girdle, dorsal aspect.
A. P., anterior projection of basipterygium; *R. A. P.*, its ridge *L. P.*, lateral process. *M. R.*, median dorsal ridge. *P. P*, posterior process. *B. V. P.*, base of ventral process.

phism in the pelvic region, a male specimen of *Corydoras nattererii* was superficially examined. The girdle and myology shown in FIGURES 26, 58, 61, and 62 are both taken from *C. paleatus*. The girdle is very small (FIGURE 26), but well ossified. It is a very aberrant type; there are no foramina and no anterior processes. The basal plate merely extends forward and ends in a somewhat lobate region, the anterior projection (*A. P.*). The lateral processes are comparatively large, ossified, and lobate in shape (*L. P.*). The two halves of the girdle form an angle with each other in the mid-line with the apex directed dorsally. That is to say, when the girdle is viewed from the dorsal aspect it has the appearance of a tent. This construction obviates the necessity of a ventral concavity. The posterior processes are also lobate, and at their base there is a small, rod-like, ventrally directed process, the

ventral process (FIGURE 61, *V. P.*), which serves as the point of attachment of the retractor ischii. The posterior processes are directed postero-laterally, rather than laterally, as in the case of other forms. On the dorsal side of the plate there is a pair of ridges (*R. A. P.*) extending from the main part of the plate into the anterior projection. Examination of the male specimen proved that there was very little sexual dimorphism. Pelvics are six-rayed; the first ray is stout and unbifurcated but not stiffened to form a spine.



FIGURES 27 and 28 *Diplomystes papillosus.* Pelvic girdle. FIGURE 27, ventral aspect FIGURE 28, dorsal aspect.

E P, external anterior process of basipterygium. *I. P.*, internal anterior process *L. P*, lateral process. *P. P*, posterior process. *Pt. M*, processus medialis (vestigial). *M S.*, median suture. *N. F.*, neural foramen.

Diplomystes papillosus

Diplomystes is accredited upon almost every basis with being the most primitive genus of all the nematognaths. It was impossible to obtain a specimen of this form, but Dr. Norman of the British Museum was kind enough to make drawings of the pelvic girdle of a prepared skeleton in his collection. These drawings are reproduced in FIGURES 27 and 28. He also sent the information that the girdle was poorly preserved; therefore, some structures of this girdle may be misinterpreted. The main body of the basipterygium is short compared to other forms. There is apparently a cartilaginous strip in the mid-line. The anterior processes are well developed, long, rod-like, and extend upon the plate forming ridges upon the ventral surface. There is a third ridge (*Pt. M.*) on the ventral surface, which courses from the center of the plate antero-medially along the anterior edge of the plate. There seems to be a small broad posterior process (*P. P.*) in the dorsal view, but it does not show plainly in the ventral view; this process,

if present, is a rudimentray one. There is no lateral process, although the postero-lateral corner of the plate (*L. P.*) is somewhat produced.

From the drawings made by Dr. Norman it would appear that the pelvic fins of *Diplomystes* are six-rayed.

MYOLOGY

Ameiurus nebulosus

The musculature of the ameiurid pelvis is rather generalized, and somewhat primitive (FIGURES 29 and 30).

The arrector ventralis is a very poorly defined muscle, and is really little more than a slip of the abductor superficialis. In fact, the tendon of the former unites with the aponeurosis by means of which the latter inserts upon the heads of the fin-rays. The slip originates on the ventral side of the ridge of the external process, and on the membrane which is stretched between this process and the internal process. It inserts ventro-laterally upon the head and shank of the first ray.

The arrector dorsalis is a clearly defined muscle, more or less cylindric in shape, originating upon the outer side of the external process of the basipterygium, and inserting dorso-laterally upon the head and shank of the first ray.

The abductor superficialis originates in the mid-line fascia and on the anterior part of the ventral surface of the basipterygium. It inserts superficially upon the heads of rays 1 to 8 inclusive.

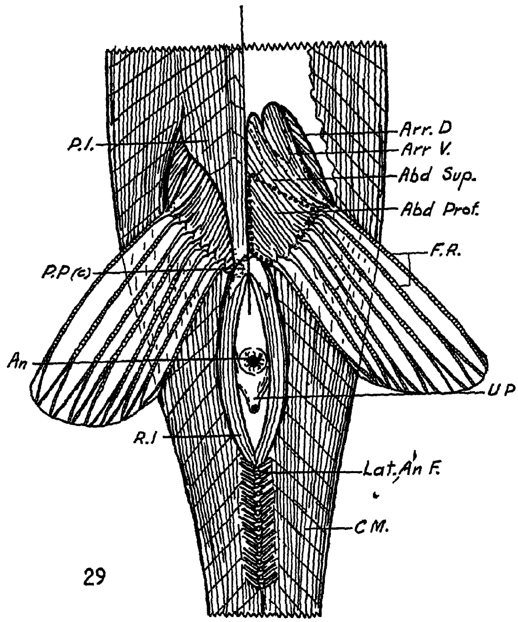
The abductor profundus originates on the posterior part of the ventral surface of the plate. It is completely covered by the superficialis, and has a deep insertion upon the heads of rays 2 to 8 inclusive.

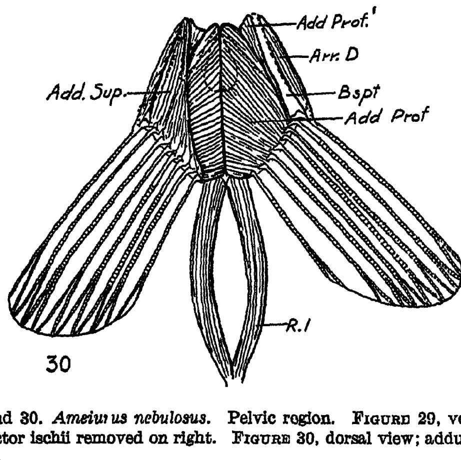
The protractor ischii originates as a slip of the great ventral muscle, and inserts by means of a tendon upon the ventral surface of the posterior process.

The retractor ischii is a long rope-like muscle, originating in part upon the basal elements of the anal fin, and in part as a slip of the third portion of the supracarinales. It inserts upon the posterior processes and upon the posterior end of the body of the plate.

All of the above muscles are shown in FIGURE 29.

The adductor superficialis is a broad, flat muscle originating upon the dorsal surface of the external process of the basipterygium, especially at the distal end of this process, and on the antero-lateral edge of the plate. It inserts superficially on the dorsal processes of rays 1 to 8 inclusive.





FIGURES 29 and 30. *Ameiurus nebulosus.* Pelvic region. FIGURE 29, ventral view, skin removed; protractor ischii removed on right. FIGURE 30, dorsal view; adductor superficialis removed on right.

Bspt., basipterygium. *Abd. Prof.*, abductor profundus. *Abd. Sup.*, abductor superficialis. *Add. Prof.*, adductor profundus. *Add. Sup.*, adductor superficialis. *Arr. D.*, arrector dorsalis. *Arr. V.*, arrector ventralis. *P. I.*, protractor ischii. *R. I.*, retractor ischii *P. P.* (*c*), posterior process (cartilaginous). *An.*, anus. *U. P.*, urogenital papilla. *F. R*, fin-rays. *Lat An F.*, lateral anal fin-muscles *C. M*, caudal myotomes

The adductor profundus is divided into two semi-independent slips (*Add. Prof.*, *Add. Prof.'*). They originate upon the dorsal surface of the basal plate, the former primarily upon the interspinous membrane between the internal and external processes. The first slip inserts deeply on the head of the second ray, while the second slip inserts deeply upon the dorsal processes of rays 2 to 8 inclusive.

Both of the muscles discussed in the two preceding paragraphs appear in FIGURE 30.

The posterior myotomes insert slightly along the postero-lateral edge of the basipterygium in the region where the fins pierce the body-wall.

Hexanematichthys (Galeichthys) felis

The pelvic musculature of this form is exceedingly complex and highly specialized (FIGURES 31–33). The muscles are very heavy and several of them are divided into a number of independent slips.

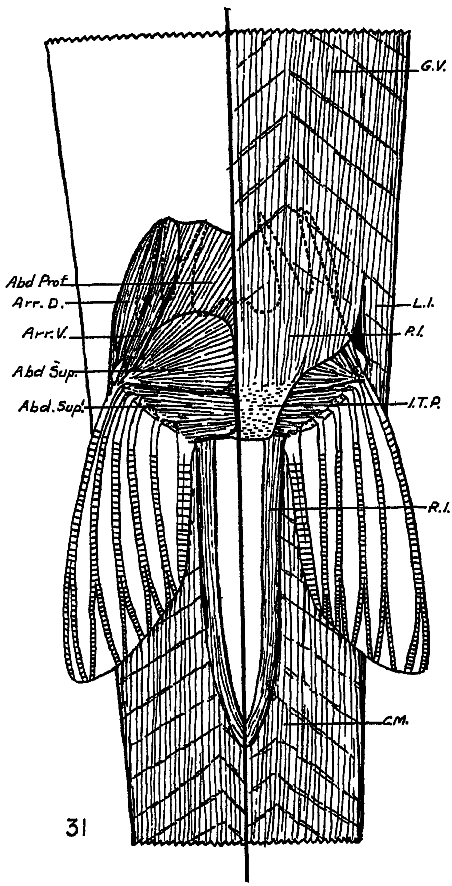
The arrector ventralis is a long, almost cylindric muscle. It originates on the inner side of the ridge of the external process, and is especially well attached at the anterior end of this process. The insertion is antero-ventral upon the head of the first ray.

The arrector dorsalis is divided into two slips. One originates on the outer ridge of the external process along its whole length. The other has the same origin, except that it is better attached on the anterior third of the ridge of the external process. They both insert upon the head and shank of the first ray, one inserting more laterally than the other.

The abductor superficialis is a complex muscle composed of a superficial fan-like slip (FIGURE 31, *Abd. Sup.*), and a deeper slip of similar character, whose posterior part is very heavy and is partially divided into semi-independent slips, each inserting upon a different ray (*Abd. Sup.'*). The superficial part of the muscle has its origin in the mid-line fascia. It inserts upon the shank of the first ray in a ventro-lateral position. The deeper part originates in the mid-line. The anterior part, which lies beneath the superficial slip, inserts laterally on the second ray. The posterior part inserts superficially upon the ventral processes of the heads of rays 2 to 6 inclusive. The portion of this posterior slip which inserts upon the clasper-ray is more or less separated from the remainder of this slip of the muscle, and is slightly heavier than the rest of the posterior portion of this muscle.

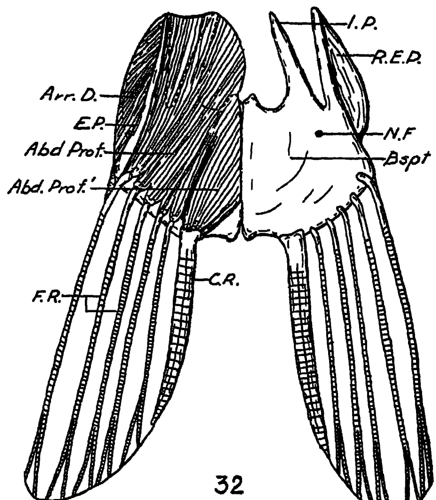
The abductor profundus is a heavy broad muscle, which originates upon the ventral surface of the pelvis and also the interspinous mem-

brane. It inserts upon rays 2 to 6 inclusive, but the portion which inserts upon the sixth ray or clasper-ray is extremely well developed, heavier than the remainder of the muscle, and more or less independent of it. The muscles discussed above are shown in FIGURE 32, while those in the preceding paragraph are presented in FIGURE 31.

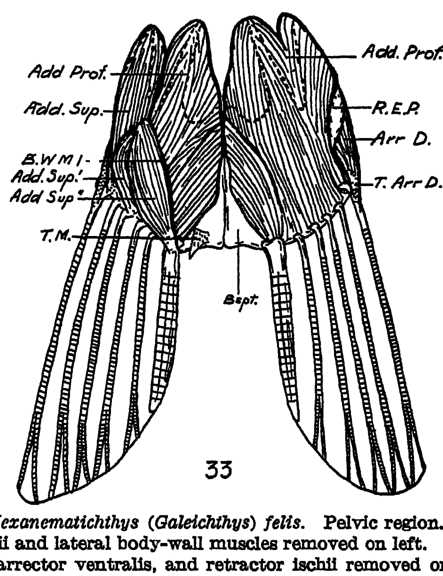


31

The adductor superficialis (*Add. Sup.*) is divided into three slips which are absolutely independent. One of these inserts upon the clasper-ray, and has its origin at a point on the basal plate where the internal and external processes meet. A second originates upon the anterior tip of the external process and inserts upon the dorsal processes (superficially) of the heads of rays 1 and 2. The third lies between the other two.



32



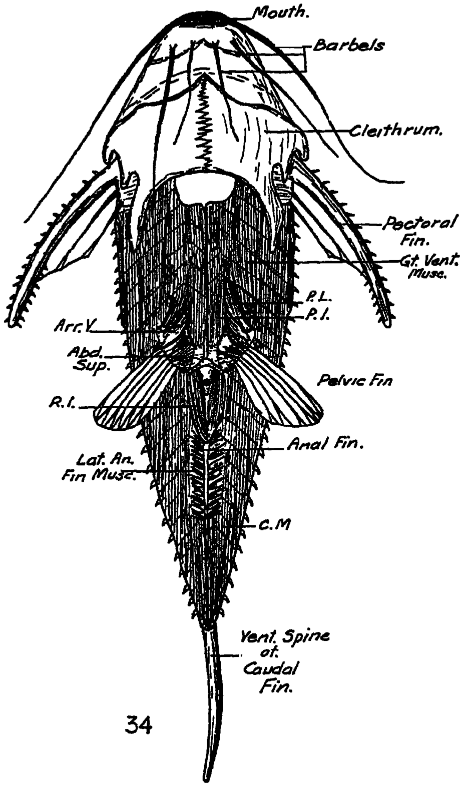
33

FIGURES 31–33. *Hexanematichthys* (*Galeichthys*) *felis*. Pelvic region. FIGURE 31, ventral view; protractor ischii and lateral body-wall muscles removed on left. FIGURE 32, same; abductor superficialis, arrector ventralis, and retractor ischii removed on left; all muscles removed on right. FIGURE 33, dorsal view; abductor superficialis removed on right.

Bspt., basipterygium. *E. P.*, external process; *R. E. P.*, its ridge. *I. P.*, internal process. *N. F.*, neural foramen. *T. M.*, tendon muscularis (insertion of myotomes). *Abd. Prof.*, abductor profundus. *Abd. Sup.*, abductor superficialis. *Add. Prof.*, adductor profundus. *Add. Sup.*, adductor superficialis. *Arr. D.*, arrector dorsalis; *T. Arr. D.*, its tendon. *Arr. V.*, arrector ventralis. *G. V.*, great ventral muscle. *L. I.*, lateral myotomes. *P. I.*, protractor ischii; *I. T. P.*, its inserting tendon. *R. I.*, retractor ischii. *B. W. M.*, body-wall muscle. *C. M.*, caudal myotomes. *C. R.*, clasper ray. *F. R.*, fin-rays.

The adductor profundus originates on the dorsal face of the basal plate and upon the interspinous membrane. It inserts deeply upon the heads of rays 1 to 6 inclusive, and again the portion of the muscle inserting upon the clasper-ray is differentiated and somewhat independent.

The dorsal muscles of this pelvis are shown in FIGURE 33.



34

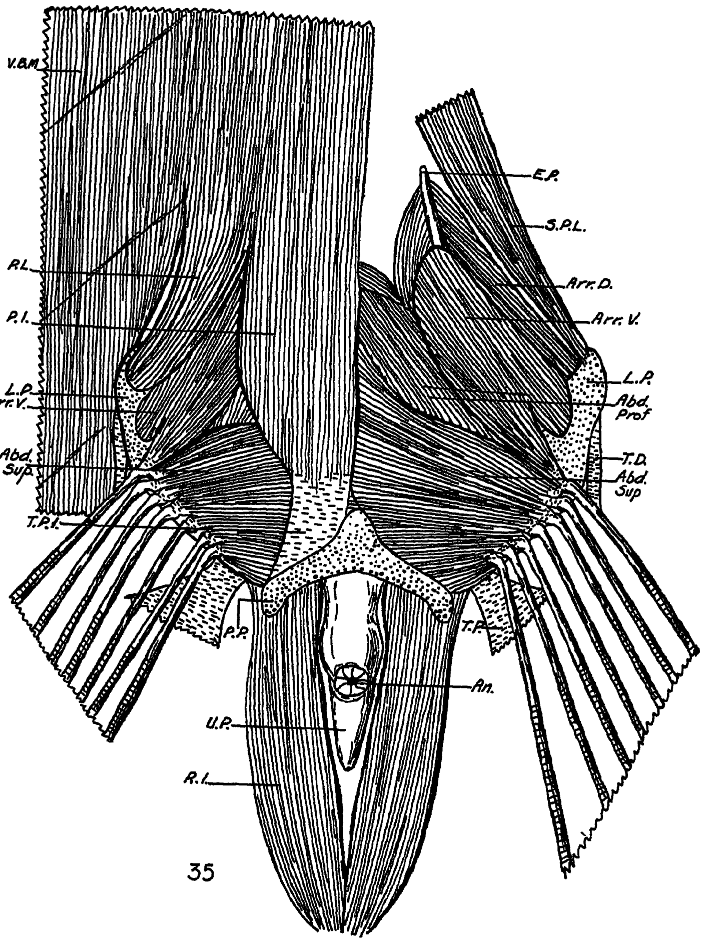
The protractor ischii, in this case, is a broad slip of the great ventral muscle, and inserts upon the posterior border by means of a well developed tendon.

The retractor ischii is a long thin muscle originating as a slip of the third portion of the supracarinales, and inserting upon the posterior edge of the basal plate.

The lateral body-wall muscles insert upon the dorsal side of the basal plate at its posterior edge by means of an extremely well developed tendon (FIGURE 33, *T. M.*).

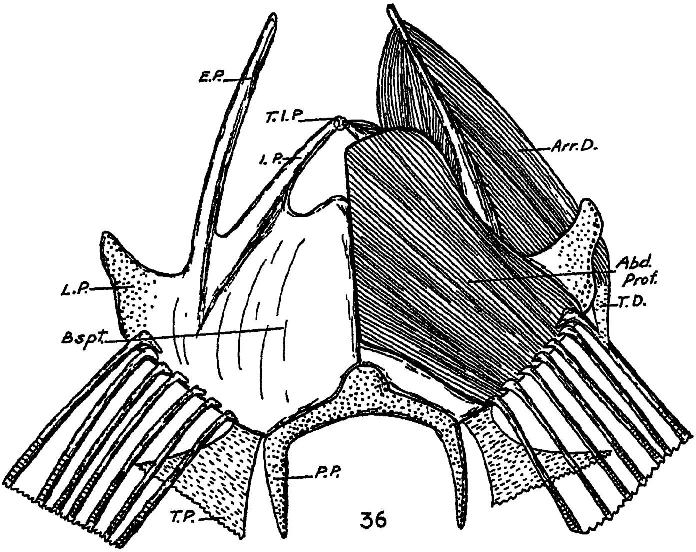
Doras hancocki

The myology of this form is depicted in FIGURES 34–37.

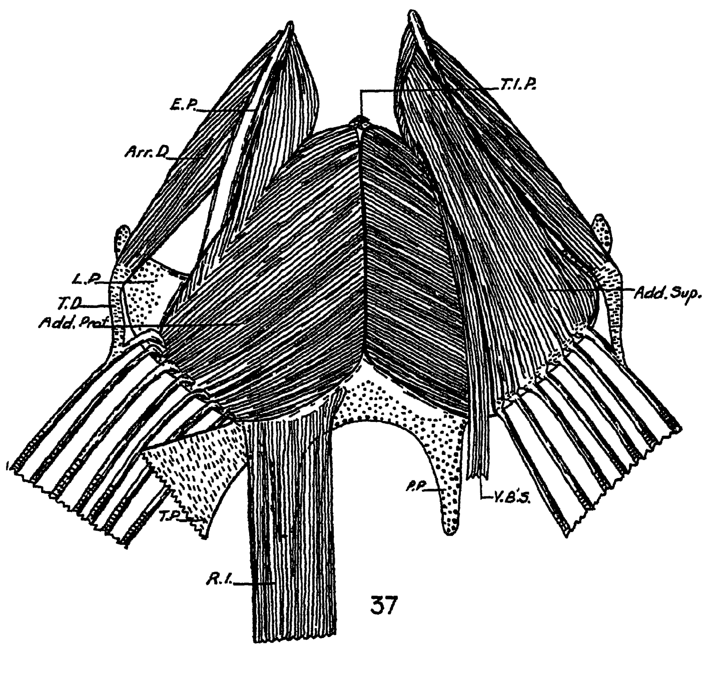


FIGURES 34 and 35. *Doras hancocki.* FIGURE 34, ventral view, skin removed. FIGURE 35, ventral view of pelvic region; protractor ischii, protractor lateralis, and lateral body-wall muscles removed on right.

E. P., external process of basipterygium. *L. P.*, lateral process. *P. P.*, posterior process. *Gt. Vent. Musc.*, great ventral muscle. *V. B. M.*, ventral body-wall muscles; *T. P.*, tendon posterior (insertion of body-wall muscles). *P. L.*, protractor lateralis. *S. P. L.*, subprotractor lateralis. *Abd. Prof.*, abductor profundus. *Abd. Sup.*, abductor superficialis. *Arr. D.*, arrector dorsalis; *T. D.*, its tendon. *Arr. V.*, arrector ventralis. *P. I.*, protractor ischii; *T. P. I.*, its inserting tendon. *R. I.*, retractor ischii. *An.*, anus. *U. P.*, urogenital papilla. *Lat. An. Fin. Musc.*, lateral anal fin-muscles. *C. M.*, caudal myotomes.


E.P.
T.I.P.
I.P.
Arr.D.
Abd. Prof.
L.P.
T.D.
Bspt.
P.P.
T.P.

36


T.I.P.
E.P.
Arr.D.
L.P.
T.D.
Add.Prof.
Add.Sup.
P.P.
V.B.S.
T.P.
R.I.

37

The arrector ventralis originates on the ventral surface of the external process of the plate, as well as upon the surface of the abductor profundus. In inserts superficially upon the head of the first ray by means of a well developed tendon.

The arrector dorsalis originates upon the outer side of the external process of the basipterygium, and inserts by means of a long, rope-like tendon upon the shank of the first ray. It passes through the loop formed by the lateral process and the body-wall muscles.

The abductor superficialis originates in the mid-line fascia, is broad and fan-like, and inserts superficially upon the heads of rays 1 to 7 inclusive.

The abductor profundus originates in the mid-line fascia and the ventral surface of the plate; its insertion is deep on the heads of rays 1 to 7 inclusive.

The protractor ischii inserts by means of a broad tendon upon the ventral surface of the proximal portion of the posterior process. A slip of the great ventral muscle which originates beside the protractor ischii inserts upon the lateral process and has arbitrarily been designated as the protractor lateralis. The subprotractor lateralis (*S. P. L.*) is another slip of the great ventral muscle which inserts upon the lateral process. It inserts beneath the protractor lateralis, and primarily upon the anterior edge of the lateral process. This is the only species studied in which this slip is present.

The retractor ischii is rather heavy, though still cylindrical. The insertion is upon the posterior process at its distal portion. It originates, as in other forms, partially from the supracarinales, and in part upon the basal elements of the anal fin.

The muscles discussed above are illustrated in FIGURES 34 and 35.

The adductor superficialis originates upon the face and inner surface of the external process. It inserts superficially upon the heads of rays 1 to 7 inclusive.

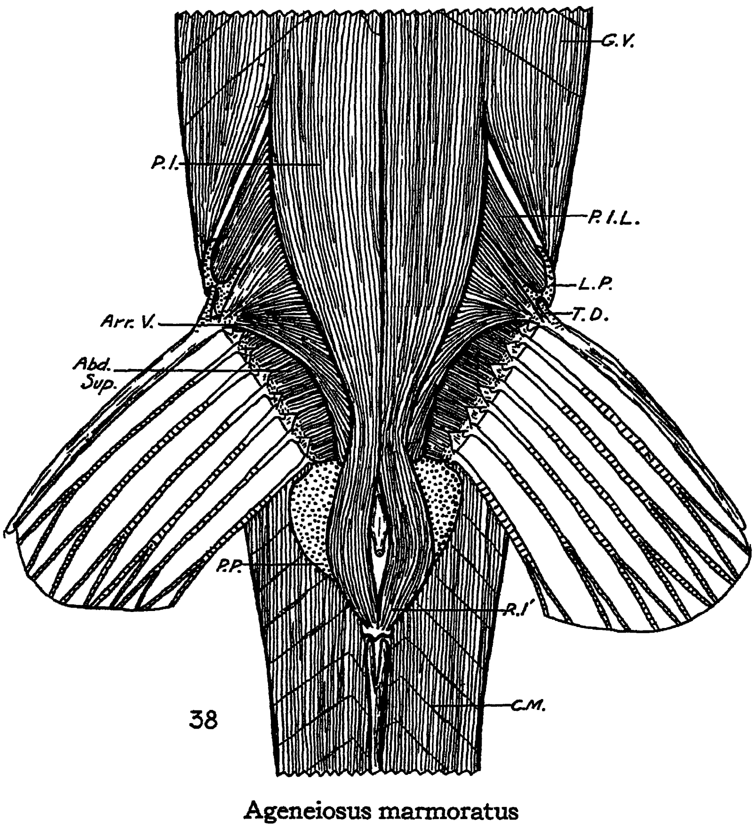
The adductor profundus is broad and divides into two slips, which are not independent. One slip originates upon the inner side of the external process of the basipterygium, and is a minor portion of this

FIGURES 36 and 37. *Doras hancocki.* Pelvic region. FIGURE 36, ventral view; abductor superficialis, arrector ventralis, and retractor ischii removed on right; all muscles removed on left. FIGURE 37, dorsal view; abductor superficialis removed on left, retractor ischii removed on right.

Bspt., basipterygium. *E. P.*, external process. *I. P.*, internal process; *T. I. P.*, tendon connecting tips of internal processes. *L. P.*, lateral process. *P. P.*, posterior process. *Abd. Prof.*, abductor profundus. *Add. Prof.*, adductor profundus. *Add. Sup.*, adductor superficialis. *Arr. D.*, arrector dorsalis; *T. D.*, its tendon. *V. B. S.*, slip of ventral body-wall muscles which inserts on basipterygium. *T. P.*, tendon posterior (insertion of body-wall muscles). *R. I.*, retractor ischii.

muscle. The second slip is the major part of the muscle, and originates upon the dorsal surface of the plate. The two slips fuse as they approach the rays; insertion being deep on the heads of rays 2 to 7 inclusive.

The above muscles are shown in FIGURE 37. In this figure, it may also be noted that the ventral body-wall myotomes insert upon the dorsal surface of the plate (*V. B. S.*).



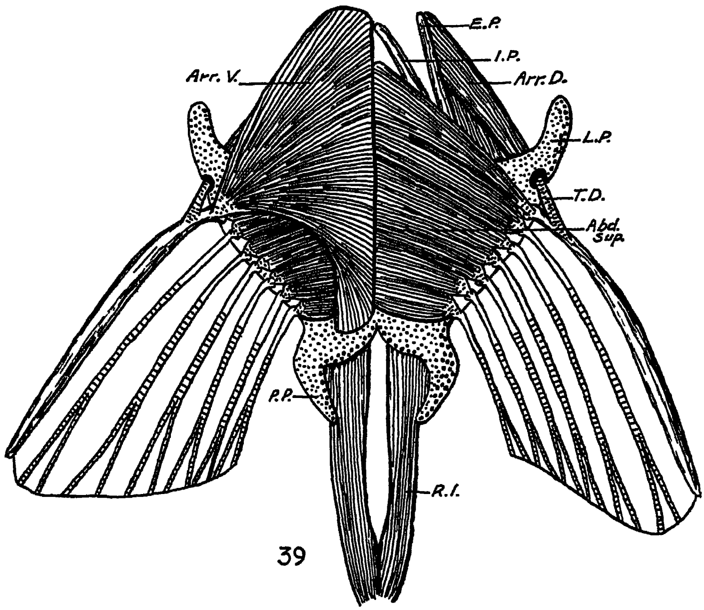
Ageneiosus marmoratus

The arrector ventralis is an extremely broad, fan-like muscle. It originates in the mid-line, as well as upon the lateral and ventral surfaces of the external process, and covers the major portion of most of the other ventral pelvic muscles. It inserts ventro-laterally upon the head and slightly upon the shank of the first ray.

The arrector dorsalis is a long, narrow muscle originating upon the external process—the anterior part. It has an extremely well devel-

oped tendon which has cut into the lateral process, and inserts laterally upon the shank of the first ray.

The abductor superficialis originates upon the face of the plate in the median area and inserts superficially upon rays 1 to 7 inclusive. It is divided into seven semi-independent slips which insert, each on a



FIGURES 38 and 39. *Ageneiosus marmoratus.* Pelvic region. FIGURE 38, ventral view. FIGURE 39, same; arrector ventralis removed on right; abductor profundus not shown, but co-extensive with abductor superficialis, beneath which it lies. (The dorsal pelvic musculature is the same as that of *Doras hancocki*, FIGURE 37.)

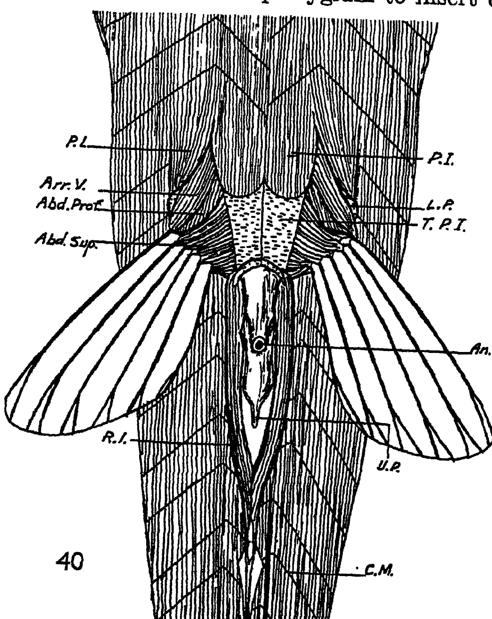
E. P., external anterior process of basipterygium. *I. P.*, internal anterior process. *L. P.*, lateral process. *P. P.*, posterior process. *G. V.*, great ventral muscle. *Abd. Sup.*, abductor superficialis. *Arr. D.*, arrector dorsalis; *T. D.*, its tendon. *Arr. V.*, arrector ventralis. *P. I.*, protractor ischii. *P. I. L.*, protractor ischii lateralis. *R. I.*, retractor ischii. *R. I.'*, projection of protractor ischii. *C. M.*, caudal myotomes.

separate ray, by means of an independent tendon, *i. e.*, each slip has its own tendon.

The abductor profundus is co-extensive with the superficialis, and like the latter, is completely divided into semi-independent slips. These slips may be under or mingled with those of the superficialis. The only criterion upon which the presence of two muscles, that is a superficialis and a profundus, may be postulated, is that two muscle-slips insert upon each ray, one having the characteristic superficial

insertion of the superficialis, the other inserting deeply as is customary with the profundus.

The protractor ischii, in this case, apparently does not insert upon the ventral surface of the posterior process, but rather, is produced past the posterior end of the basipterygium to insert upon the basal

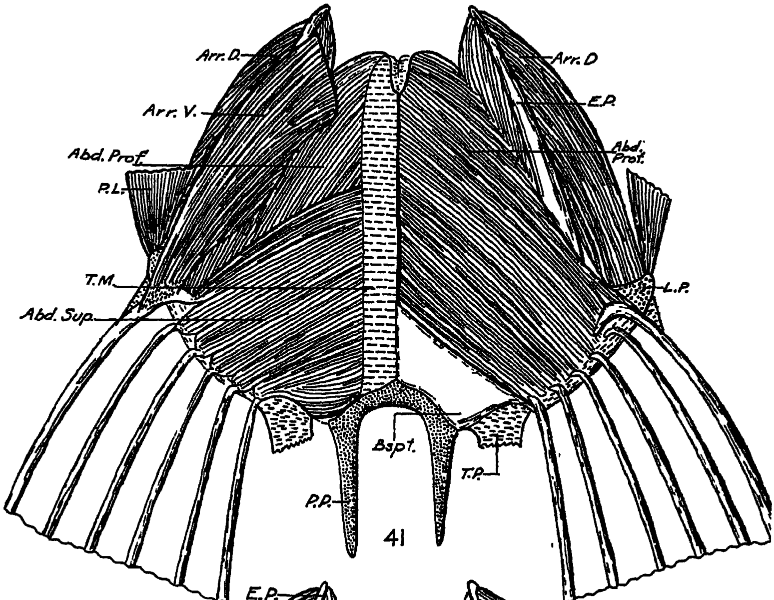


FIGURES 40–42. *Rhamdia* sp. Pelvic region. FIGURE 40, ventral view. FIGURE 41, same; abductor superficialis and arrector ventralis removed on right. FIGURE 42, dorsal view; adductor superficialis removed on left.

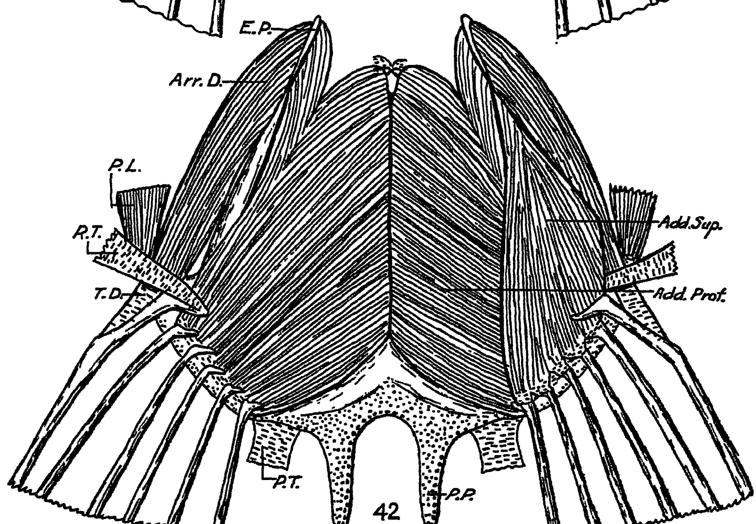
Bspt., basipterygium. *E. P.*, external anterior process. *L. P.*, lateral process. *P. P.*, posterior process. *T. M.*, tendon medialis, connecting the tips of the internal anterior processes. *Abd. Prof.*, abductor profundus. *Abd. Sup.*, abductor superficialis. *Add. Prof.*, adductor profundus. *Add. Sup.*, adductor superficialis. *Arr. D.*, arrector dorsalis; *T. D.*, its tendon. *Arr. V.*, arrector ventralis. *P. I.*, protractor ischii; *T. P. I.*, its inserting tendon. *P. L.*, protractor lateralis. *R. I.*, retractor ischii. *R. T.*, tendon inserting on head of first ray. *T. P. (P. T.)*, tendon posteriosus, insertion of caudal myotomes. *C. M.*, caudal myotomes. *An.* anus. *U. P.*, urogenital papilla.

elements of the anal fin. The protractor lateralis is present and is similar, in its relationships to other pelvic structures, to the subprotractor lateralis in *Doras hancocki*, since it originates from the body of the great ventral muscle beneath the origin of the protractor ischii rather than beside the origin of the protractor ischii as is the case with the protractor lateralis in *Doras*. There is no muscle-slip in this form which is analagous to this latter muscle in *Doras*.

The retractor ischii, in this form, runs dorsal to the posterior projection of the protractor between the basipterygium and the anal fin.



41



42

However it does not insert upon the posterior process but rather upon the posterior end of the plate.

The myology of *Ageneiosus* is shown in FIGURES 38 and 39.

The dorsal myology of the pelvis in this species is the same as that of *Doras hancocki.*

Rhamdia sp.

The myology of *Rhamdia* is almost the exact counterpart of that of *Doras* except that there is no subprotractor lateralis. As in the case

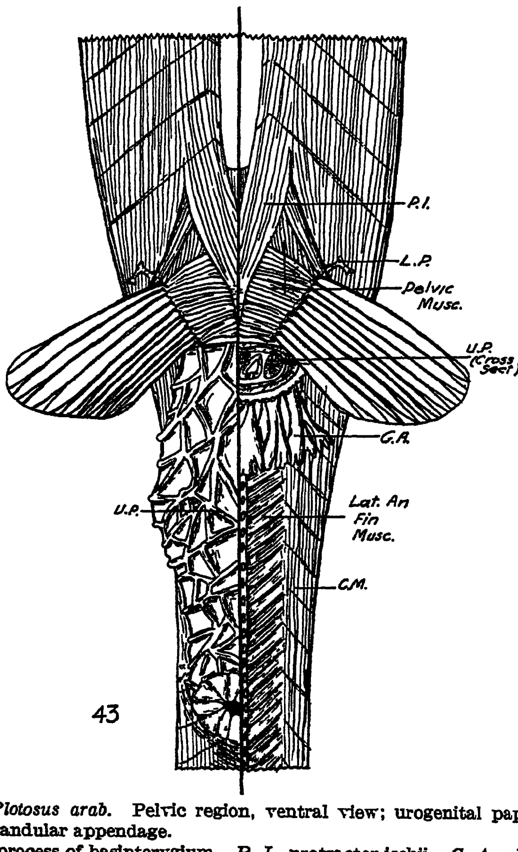


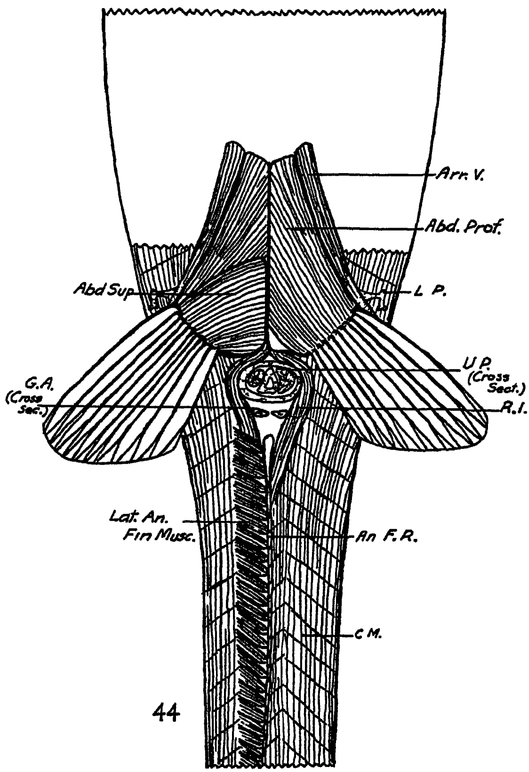
FIGURE 43. *Plotosus arab.* Pelvic region, ventral view; urogenital papilla removed on right, to show glandular appendage.

L. P., lateral process of basipterygium. *P. I.*, protractor ischii. *G. A.*, glandular appendage. *Lat. An. Fin. Musc.*, lateral anal fin-muscles. *C. M.*, caudal myotomes. *U. P.*, urogenital papilla.

of *Doras*, there is a slip of the great ventral muscle, the protractor lateralis, which inserts upon the lateral process of the basipterygium. One difference is that the retractor ischii originates solely upon the basal elements of the anal fin. The dorsal aspect is different only in

the fact that there is a tendon which inserts upon the dorsal process of the head of the first ray. Anterior traction upon this tendon causes the first ray to move dorsally, posterior traction causes ventral movement of the ray.

The myology of this form will be found in FIGURES 40, 41, and 42.



44

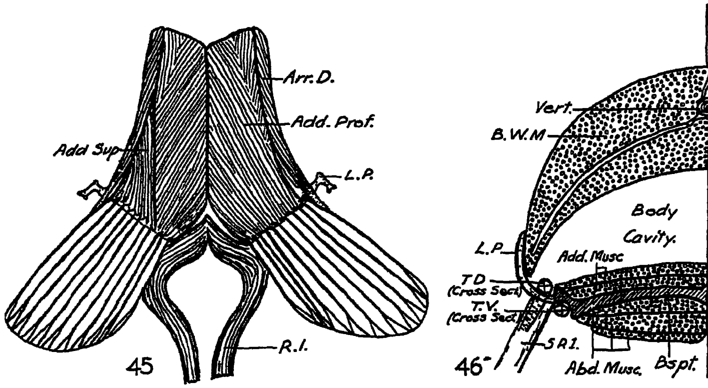
FIGURE 44. *Plotosus arab.* Pelvic region, ventral view; urogenital papilla removed, and lateral body-muscles and protractor ischii removed on right.

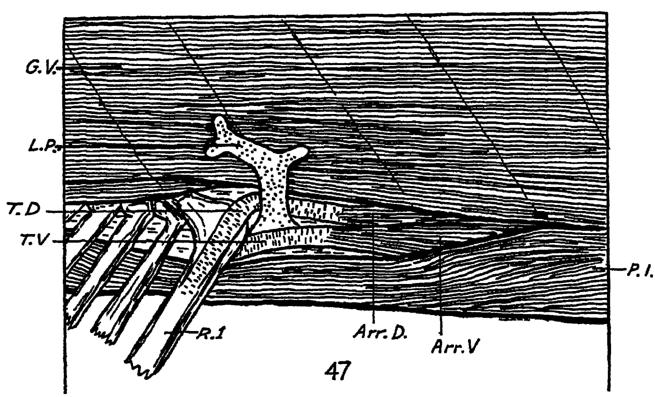
L. P., lateral process of basipterygium. *Abd. Prof.*, abductor profundus. *Abd. Sup.*, abductor superficialis. *Arr. V.*, arrector ventralis. *R. I.*, retractor ischii. *Lat. An. Fin Musc.*, lateral anal fin-muscles. *An. F. R.*, anal fin-rays. *C. M.*, caudal myotomes. *G. A.*, glandular appendage. *U. P.*, urogenital papilla.

Plotosus arab

This form has the usual complement of six muscles upon the pelvis, namely: arrector ventralis, arrector dorsalis, abductor superficialis, abductor profundus, adductor superficialis, adductor profundus.

The protractor ischii, however, inserts in the mid-line of the pos-



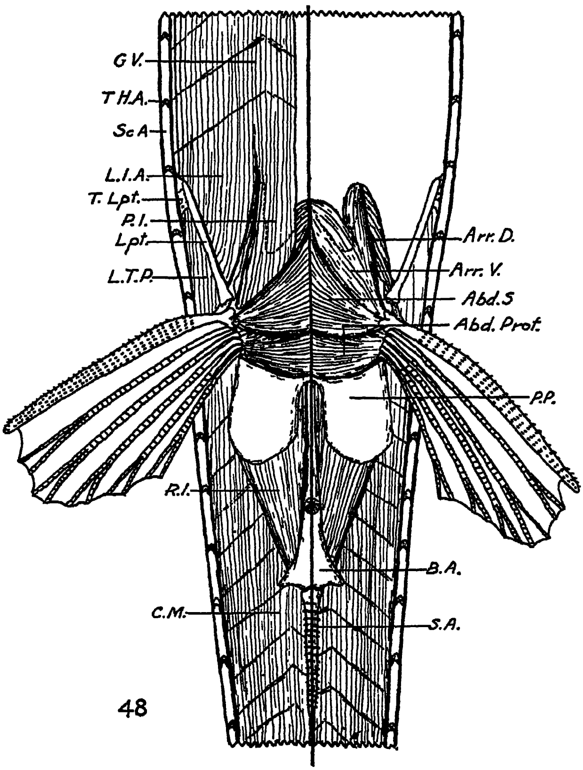


FIGURES 45–47. *Plotosus arab.* FIGURE 45. dorsal view of pelvic region; adductor superficialis removed on right. FIGURE 46, hypothetical cross-section of body through the insertion of body-wall muscles on lateral process, showing pulley-arrangement. FIGURE 47, semi-diagrammatic lateral view of pelvic region, showing relations between the lateral process, the tendon of the arrector dorsalis, and the body-wall muscles which make possible the pulley-arrangement.

Vert., vertebra. *Bspt.*, basipterygium. *L. P.*, lateral process. *Abd. Musc.*, abductor muscles. *Add. Musc.*, adductor muscles. *Add. Prof.*, adductor profundus. *Add. Sup.*, adductor superficialis. *Arr. D.*, arrector dorsalis; *T. D.*, its tendon. *Arr. V.*, arrector ventralis; *T. V.*, its tendon. *B. W. M.*, body-wall muscles. *G. V.*, great ventral muscle. *P. I.*, protractor ischii. *R. I.*, retractor ischii.

terior portion of the plate. There is no protractor lateralis. (FIGURES 43–47.) Since there are no posterior processes, the retractor ischii

inserts directly upon the posterior part of the basipterygium, primarily on the dorsal part.



48

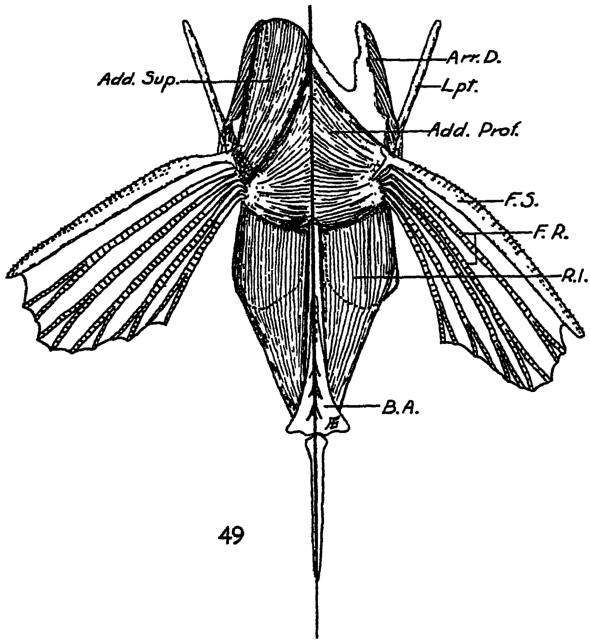
FIGURE 48. *Pterygoplichthys anisitoi.* Pelvic region, ventral view; ventral body-armor removed, protractor ischii and lateral body-wall muscles removed on right.

Sc. A., scutes of body-armor; *T. H. A.*, one of their tendonous hinges. *Lpt.*, lateropterygium; *T. Lpt.*, tendon by which it is attached distally to body-armor. *P. P.*, posterior process. *B. A.*, basal element of anal fin. *S. A.*, spine of anal fin. *G. V.*, great ventral muscle; *L. I. A.*, its lateral, inserting on basipterygium. *Abd. Prof.*, abductor profundus. *Abd. Sup.*, abductor superficialis. *Arr. D.*, arrector dorsalis. *Arr. V.*, arrector ventralis. *P. I.*, protractor ischii. *R. I.*, retractor ischii. *C. M.*, caudal myotomes.

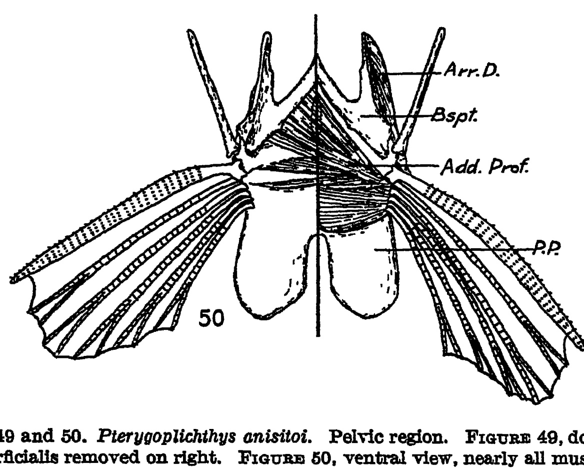
Pterygoplichthys anisitoi

In *Pterygoplichthys*, the purely pelvic muscles are of the general type and arrangement; however, there is one important difference.

In the case of the abductor profundus (FIGURE 50) the whole muscle is divided into a large number of independent slips, some of which

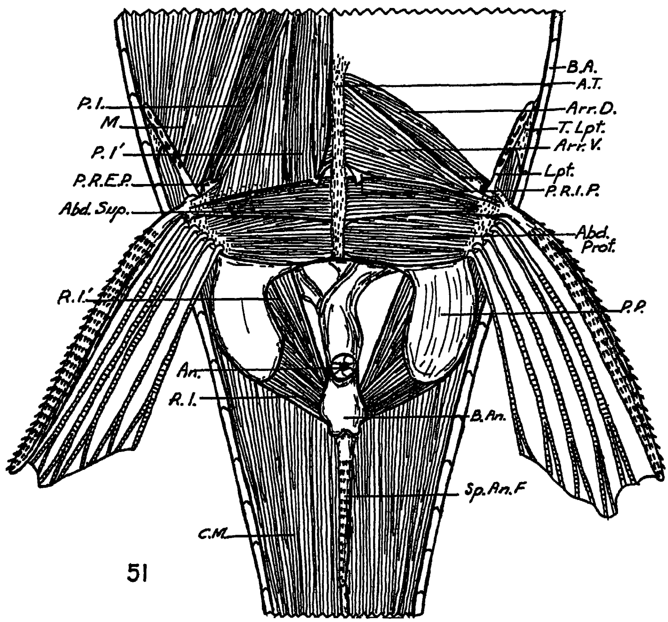


49

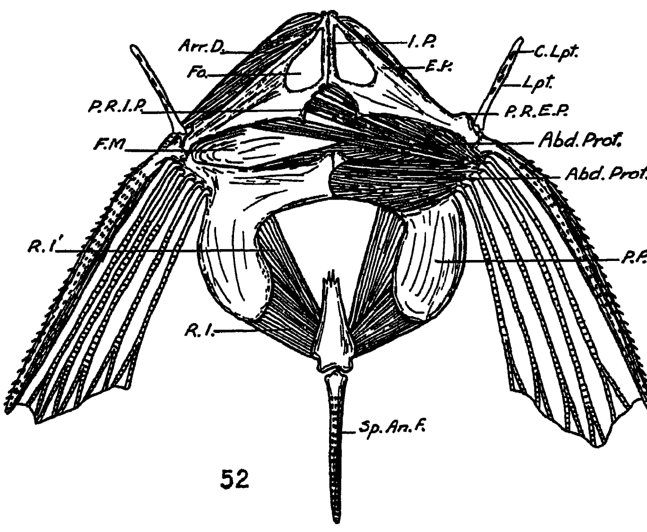


50

FIGURES 49 and 50. *Pterygoplichthys anisitoi.* Pelvic region. FIGURE 49, dorsal view; adductor superficialis removed on right. FIGURE 50, ventral view, nearly all muscles removed. *Bspt.*, basipterygium. *Lpt.*, lateropterygium. *P. P.*, posterior process. *F. S.*, fin-spine. *F. R.*, fin-ray. *B. A.*, basal element of anal fin. *Abd. Prof.*, abductor profundus. *Add. Prof.*, adductor profundus. *Add Sup.*, adductor superficialis. *Arr. D.*, arrector dorsalis. *R. I.*, retractor ischii.



51



52

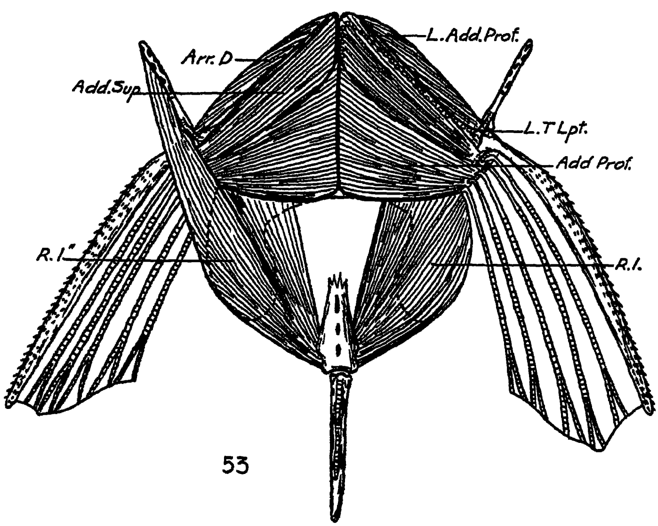
FIGURES 51 and 52. *Xenocara chagresi.* Pelvic region, ventral view. FIGURE 51, ventral body-armor removed; protractor ischii and anterior myotomes removed on right. FIGURE 52, all muscles except arrector dorsalis and retractor ischii removed on left, all except abductor profundus and retractor ischii removed on right.

B. A., body-armor. *E. P.*, external anterior process of basipterygium; *P. R. E. P.*, projection of its ridge. *I. P.*, internal anterior process; *P. R. I. P.*, projection of its ridge. *Fo.*,

lateral foramen. *A. T.*, anterior tendon; attaches pelvis to body-armor. *Lpt.*, lateropterygium; *C. Lpt.*, its canals; *T. Lpt.*, its tendon. *P. P.*, posterior process. *B. An.*, base of anal fin. *Sp. An. F.*, spine of anal fin. *F. M.*, fossa muscularis. *M.*, great ventral muscle. *Abd. Prof.*, abductor profundus. *Abd. Sup.*, abductor superficialis. *Arr. D.*, arrector dorsalis. *Arr V.*, arrector ventralis. *P. I.*, protractor ischii. *R. I.*, retractor ischii. *C. M.*, caudal myotomes. *An.*, anus.

originate upon the internal ridge of the opposite side. Since the profundus muscles of both sides make this cross-over, it is evident that the slips will intermingle. This condition is designated as decussation of the profundus. It is important to note that the anterior and posterior myotomes insert upon the lateropterygium, the retractor ischii primarily upon the posterior end of the body of the plate rather than on the posterior processes (FIGURES 48, 49, 50).

A more complete discussion of the muscles in this form will be found in the section dealing with the functions of muscles.



53

FIGURE 53. *Xenocara chagresi.* Pelvic region, dorsal view; special slip of retractor ischii removed on right; anterior border of adductor profundus shown in dotted outline.

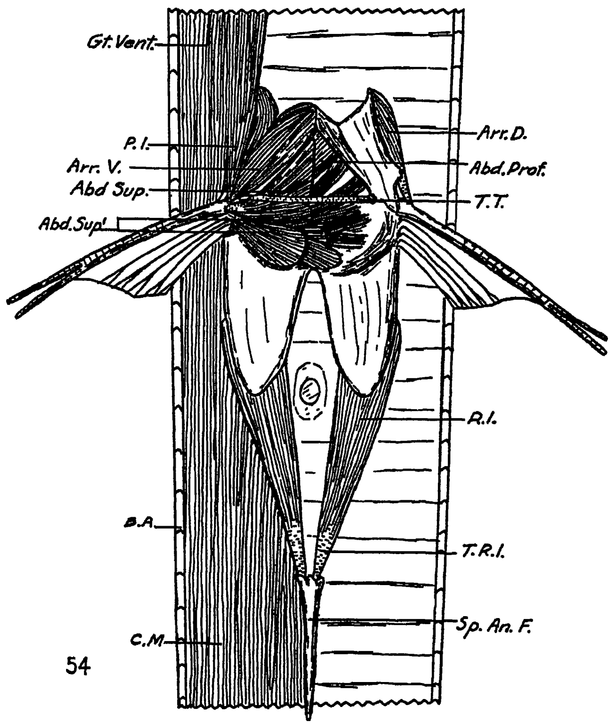
Add. Prof., adductor profundus; *L. Add. Prof.*, its anterior border, covered by adductor superficialis (*Add. Sup.*). *Arr. D.*, arrector dorsalis. *L. T. Lpt.*, lateral tendon of lateropterygium. *R. I.*, retractor ischii.

Xenocara chagresi

The myology of this form is illustrated in FIGURES 51–53.

The pelvic muscles are of the same general type as those of *Pterygoplichthys*, although they have a more transverse direction, due to the fact that the pelvis is so much shorter compared to its length.

The anterior and posterior myotomes again insert upon the lateropterygium. In the protractor ischii, which inserts upon the internal transverse ridge of the basal plate, there are differentiated two heavy strips of muscle (*P. I.* and *P. I.'*). One of these inserts upon the projection of the ridge of the internal process, the other upon the process



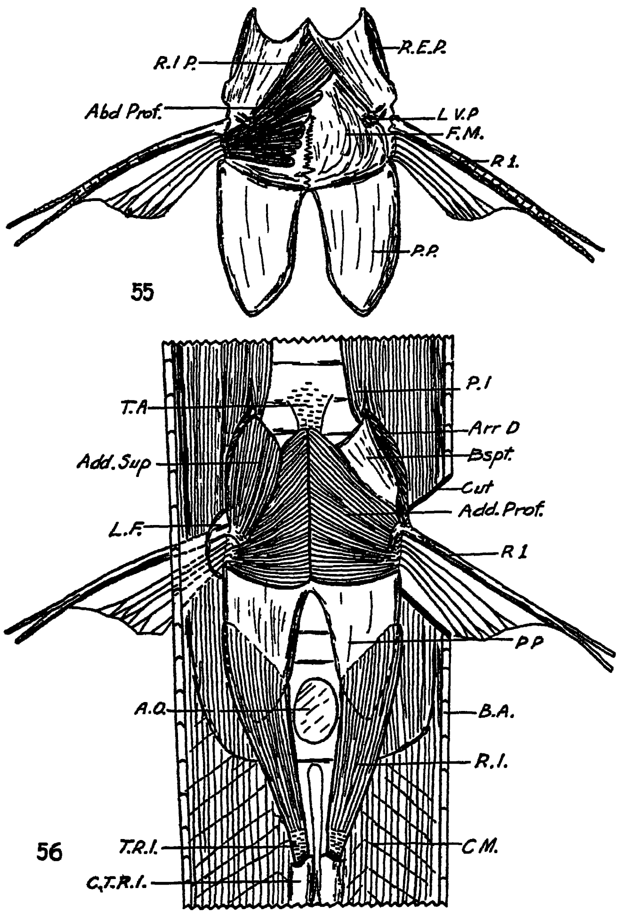
54

Figure 54. *Farlowella amazonum.* Pelvic region, ventral view; myotomes and all pelvic muscles except arrector dorsalis removed on right.

B. A., body-armor. *Gt. Vent.*, great ventral muscle. *Abd. Prof.*, abductor profundus. *Abd. Sup.*, abductor superficialis. *Arr. D.*, arrector dorsalis. *Arr. V.*, arrector ventralis. *T. T.*, transverse tendon. *P. I.*, protractor ischii. *R. I.*, retractor ischii; *T. R. I.*, its tendon. *C. M.*, caudal myotomes. *Sp. An. F.*, spine of anal fin.

or projection of the ridge of the external process (*P. R. E. P.*). The retractor ischii is also modified to form three independent slips (*R. I.'*, *R. I.*, and *R. I.''*). One of these inserts upon the posterior side of the lateropterygium, another on the dorsal side of the posterior processes,

and the third upon the posterior edge of the basal plate. There is decussation of the profundus on the ventral surface of the plate.



FIGURES 55 and 56. *Farlouella amazonum.* Pelvic region. FIGURE 55, ventral view, all muscles except left abductor profundus removed. FIGURE 56, dorsal view, abductor superficialis removed on right.

B. A, body-armor. *L. F.*, fin-ray foramen through body-armor. *A. O.*, anal foramen in body-armor. *T. A.*, anterior tendon; attaches pelvis to body-armor. *Bspt.*, basipterygium. *R. E. P.*, ridge of external process. *R. I. P.*, ridge of internal process. *L. B. P.*, lateral ventral process, serving as attachment for transverse tendon. *F. M.*, fossa muscularis. *P. P.*, posterior process. *Abd. Prof.*, abductor profundus. *Add. Prof.*, adductor profundus. *Add. Sup.*, adductor superficialis. *Arr. D.*, arrector dorsalis. *P. I.*, protractor ischii. *R. I.*, retractor ischii; *T. R. I.*, its tendon; *C. T. R. I.*, canal through which its tendon passes to spine of anal fin. *C. M.*, caudal myotomes. *R. 1*, first ray.

Farlowella amazonum

This form, represented in FIGURES 54, 55, and 56, is highly specialized in the ventral musculature. The arrector ventralis is a flat, fan-shape muscle divided into two slips at its distal end. One slip originates on the inside of the external process, the other on the outside of the ridge of the internal process. The two slips join and insert ventrolaterally on the head and shank of the first ray. The arrector dorsalis is a cylindric muscle originating on the outside of the ridge of the external process, and inserting dorso-laterally upon the head and shank of the first ray.

The abductor superficialis is divided into numerous slips, some of which originate upon the face of the plate on the other side of the midline. None of these slips is absolutely independent along its whole length, although the two main slips (FIGURE 54, *Abd. Sup.* and *Abd. Sup.'*) are united only in the region of their inserting tendon. The abductor profundus shows decussation, although it is not so pronounced as in *Pterygoplichthys.*

The dorsal aspect of the pelvic musculature is of a generalized type. The pelvis is attached to the ventral body-armor anteriorly by a tendon.

The protractor ischii is very small, and inserts upon the latero-posterior end of the ridge of the internal process. There are special canals in the body-armor through which the tendon of the retractor ischii pasess to insert upon the spine of the anal fin.

Astroblepus (Cyclopium) homodon

The ventral aspect of the musculature of the pelvis of this form (FIGURES 57 and 59) is of a rather divergent type. One of the most noticeable characteristics of this form is that none of the ventral muscles overlap each other.

The arrector dorsalis and ventralis have the same general form as in *Xenocara.*

The abductor superficialis is a small fan-shaped muscle originating upon the ventral surface of the basal plate; it inserts superficially on the head of the first ray only.

The abductor profundus is a very rudimentary muscle covering only the most posterior part of the ventral face of the basal plate. It has a deep insertion upon the heads of rays 2 to 5 inclusive.

The retractor ischii is rather flat, and inserts upon the anterior tip of the external anterior processes. This feature is worthy of note.

The protractor ischii, in this case, is no longer a slip of the great ventral muscle, but is an independent muscle originating on the posterior border of the cleithrum, and inserting upon a small ossified lateral process (FIGURE 25, *L. P.*) of the basipterygium. Furthermore, the fibers of this muscle are spiraled, and the muscle has the appearance of a twisted hemp rope.

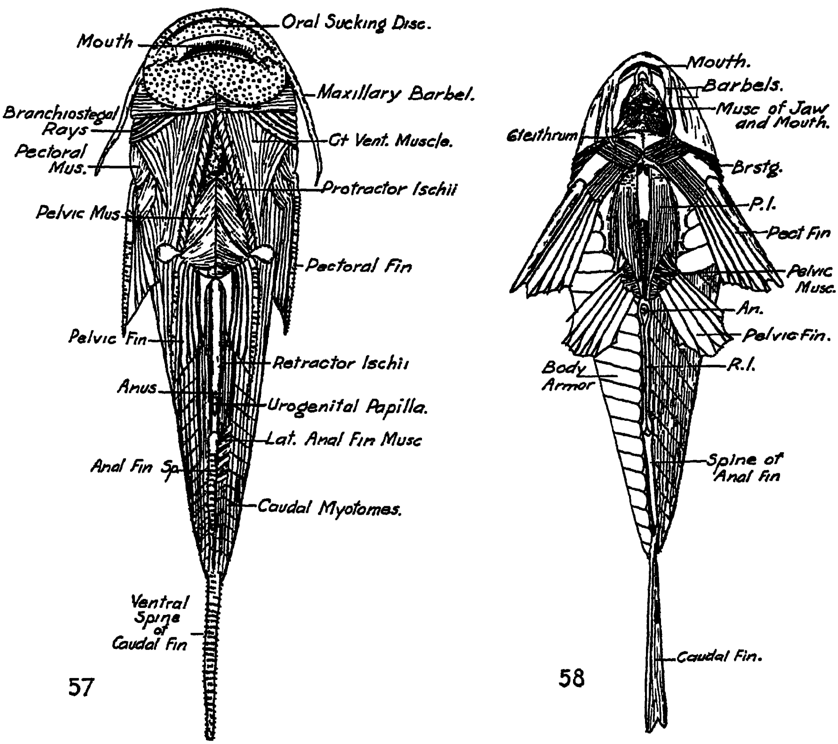


FIGURE 57. *Astroblepus homodon.* Ventral view, skin removed.
FIGURE 58. *Corydoras paleatus.* Ventral view, body-armor removed on right.
Brstg., branchiostegal rays. *Pect. Fin*, pectoral fin. *P. I.*, protractor ischii. *R. I.*, retractor ischii. *An.*, anus.

The adductor profundus is rather small, and originates in the midline fascia and dorsal face of plate; it is not overlapped by the superficialis. It inserts deeply upon the heads of rays 2 to 5 inclusive. There are two small muscles upon the dorsal surface of the plate which may be derivatives of the adductor profundus. One (FIGURE 60, *Ad. P.*) is a fan-like muscle which lies beneath the superficialis and inserts upon the head of the first ray. The second (*Ad. P.'*) is merely a slip

of the profundus which is more or less independent, and inserts upon the head of the second ray. Both of the insertions are rather intermediate, being neither deep nor superficial.

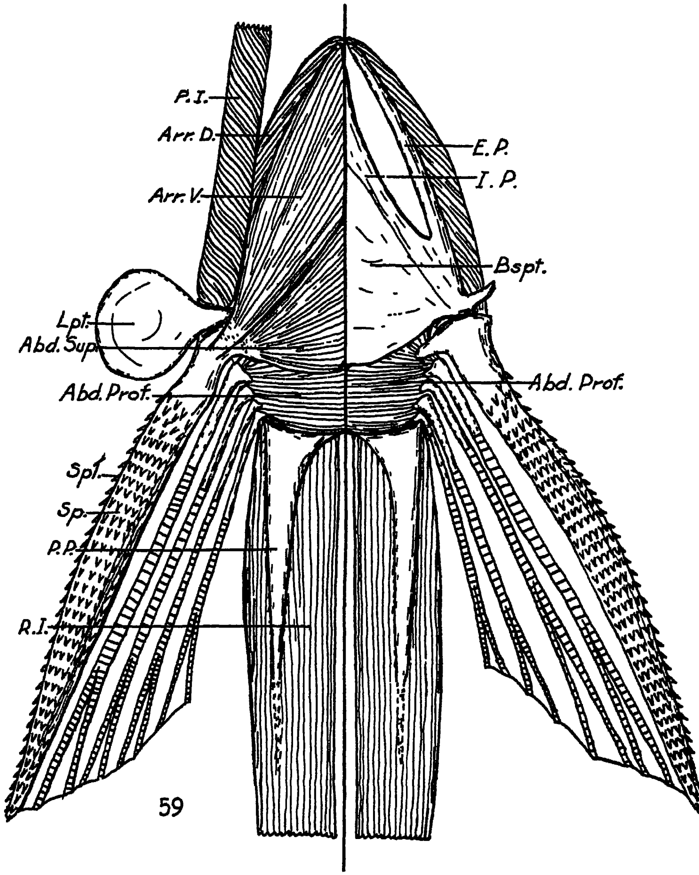


FIGURE 59. *Astroblepus homodon.* Pelvic region, ventral view; abductor superficialis and arrector ventralis removed on right.
Bspt., basipterygium. *E. P.*, external anterior process. *I. P.*, internal anterior process. *Lpt.*, lateropterygium. *P. P.*, posterior process. *Sp.*, spine. *Spl.*, spinules. *Abd. Prof.*, abductor profundus. *Abd. Sup.*, abductor superficialis. *Arr. D.*, arrector dorsalis. *Arr. V.*, arrector ventralis. *P. I.*, protractor ischii. *R. I.*, retractor ischii.

The adductor superficialis inserts only on the head of the first ray. It originates on the inner side of the external process and the outside of the internal process. It has a tendon which runs along the middle of the muscle forming its longitudinal axis. Many of the fibers insert upon this tendon.

The dorsal aspect of the myology is given in FIGURE 60.

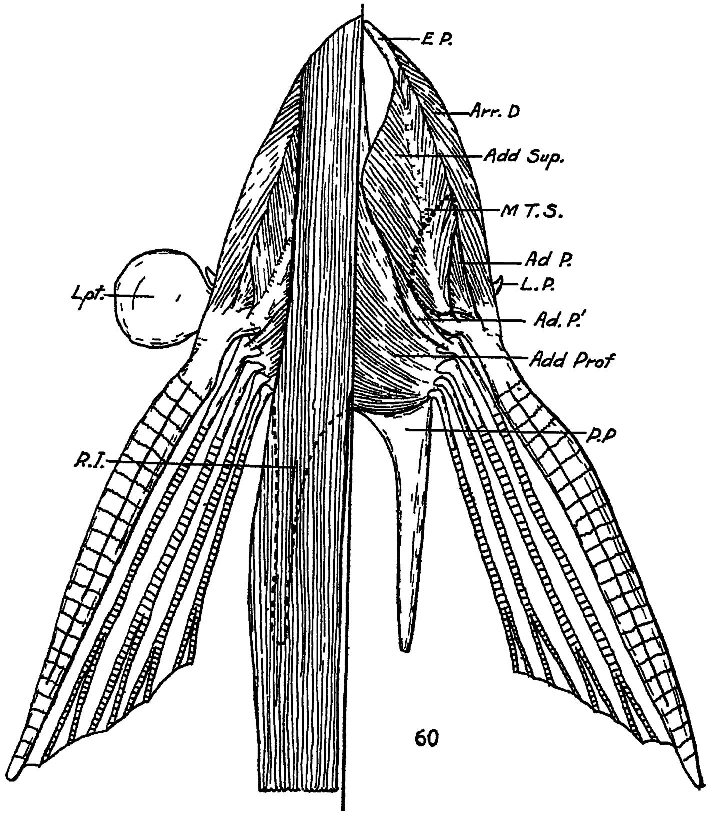


FIGURE 60. *Astroblepus homodon.* Pelvic region, dorsal view, retractor ischii removed on right

E. P., external anterior process of basipterygium. *L. P.*, lateral process. *Lpt.*, laterapterygium *P. P.*, posterior process *Add. Prof.*, adductor profundus *Add. Sup.*, adductor superficialis; *M. T. S.*, its median tendon, *Ad. P*, small independent muscle, lying beneath adductor superficialis, probably derived from adductor profundus. *Arr. S*, arrector dorsalis. *R. I.*, retractor ischii.

Corydoras paleatus

The major variation of this form from the generalized form is that the arrector dorsalis has shifted from the dorsal to the ventral side of the plate. Accompanying this change, the point of insertion has changed from a dorso-lateral one to a purely lateral, or possible a ventro-lateral position.

The abductor superficialis is a small fan-like muscle originating in the mid-line and inserting superficially upon the ventral processes of

the heads of rays 1 and 2. The origin also includes a portion of the surface of the plate at its posterior end.

The abductor profundus originates upon the ventral surface of the plate. It inserts deeply on ventral processes of the heads of rays 1 to 6 inclusive.

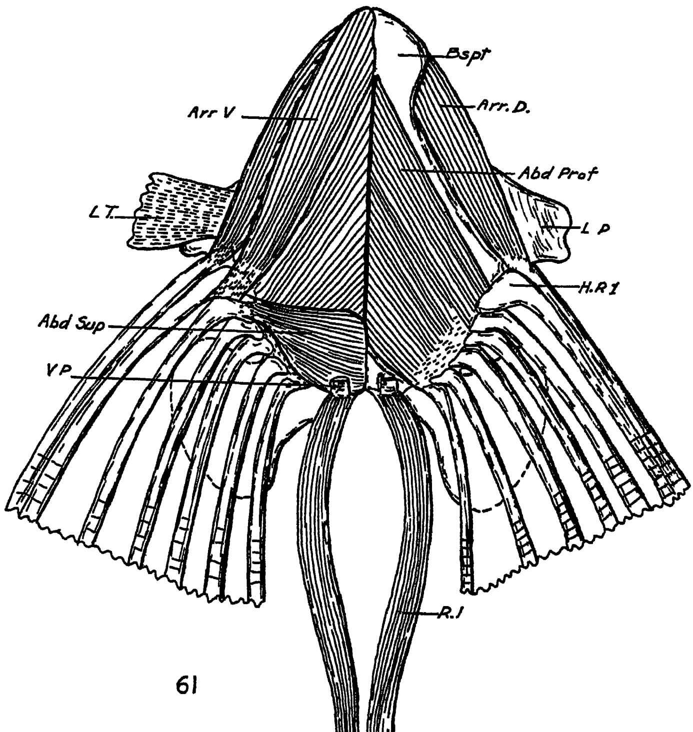


FIGURE 61 *Corydoras paleatus*. Pelvic region, ventral view; abductor superficialis and arrector ventralis removed on right.

Bspt., basipterygium. *L. P.*, lateral process *V P.*, ventral process. *L. T.*, lateral tendon. *H. R. 1*, head of first ray. *Abd. Prof.*, abductor profundus *Abd. Sup*, abductor superficialis *Arr D.*, arrector dorsalis *Arr. V.*, arrector ventralis. *R I.*, retractor ischii.

The adductor muscles are of a generalized type as may be seen on FIGURE 62. The figures illustrating the myology of this form are FIGURES 58, 61 and 62.

The retractor ischii is long, thin, and thread-like, and instead of inserting upon the posterior processes it inserts upon a pair of pro-

cesses characteristic of this form, the ventral processes (FIGURE 61, *V. P.*). The protractor ischii is a broad, flat slip of the great ventral muscle. It is very poorly developed, and probably has little effect on the pelvis. It inserts upon the posterior end of the basipterygium.

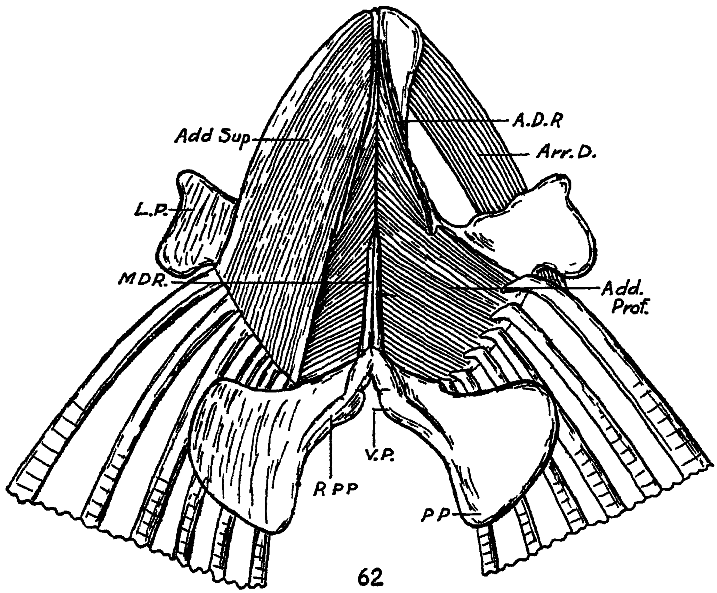


FIGURE 62. *Corydoras paleatus* Pelvic region, dorsal aspect, adductor superficialis removed on right.
L. P., lateral process of basipterygium. *P. P.*, posterior process, *R P. P*, its ridge. *V. P*, ventral process. *A D. R.*, anterior dorsal ridge. *M. D R.*, median dorsal ridge. *Add Prof*, adductor profundus. *Add. Sup.*, adductor superficialis *Arr. D.*, arrector dorsalis.

CORRELATION OF FORM AND FUNCTION

This part of the thesis will use two methods in approaching the problem of correlation of functional idiosyncrasies with morphological variations. On one hand, it will consider certain peculiar functions of the pelvic fins discussed by Breder (1935) and other authors, and show that there are morphological variations which enable the organism to carry on these activities. On the other hand, it will examine morphological variations, in forms where the habits are poorly known, and suggest hypothetic functions to which these structures might be put.

Normal Functions

It seems that a logical starting point is a discussion of the normal functions of the various pelvic muscles. This study will be taken up with *Pterygoplichthys anisitoi* (FIGURES 48–50), since this was the largest form studied, and the functions of the muscles are more easily determined. *Pterygoplichthys* has a full complement of six pelvic muscles, and these show little variation from the typical pelvic myology postulated by Grenholm (1923).

The arrector ventralis (FIGURE 48, *Arr. V.*,) when it contracts, rotates the first ray antero-ventrally, and thus draws the fin away from the body and spreads it, as explained in the discussion of the lepidotrichia. This action will bring the fin into such a position that its transverse section will be vertical, or very close to it. That is to say, the fin will form a vertical plane whose long axis is parallel to the long axis of the body. This will cause a decrease in the horizontal (lift) area of the pelvic fin, and, therefore, a drop in the caudal region. Then, thus expanded, the pelvics will act as a keel and tend to keep the body moving in a straight path, other forces being neutral. They will also help to prevent the "wiggle" consequent upon the undulatory propulsive movements of the caudal myotomes. The abductor superficialis (*Abd. S.*), in this form, inserts only on the first ray, while in most other cases it inserts on all or the majority of the rays. The difference in function is merely that all rays are actively moved in the latter case, while in the former they are passively moved by action of the first ray; the net effect on the fin is the same in both cases. The abductor superficialis draws the first ray ventro-medially or medially, thus folding the fin and bringing it close to the body. It serves as a method of lessening fin-surface and getting the fin out of the way. It decreases lift-area of the pelvic fins and causes a drop in the posterior end.

The abductor profundus (FIGURE 50, *Abd. Prof.*) rotates and draws the whole fin ventro-medially without either expanding or contracting it. It thus brings the fin from the horizontal stabilizing plane to a vertical one. In other words, it brings the fin from a position where it can direct the body up or down, to one where it serves as a keel to keep body-motion in a straight line or direct it to the right or left. It also decreases lift-area.

The arrector dorsalis (FIGURES 48–50, *Arr. D.*) draws the first ray antero-dorsally or anteriorly, depending upon the original position of the fin. It simultaneously spreads the fin, and brings it into a more or

less horizontal plane with a varying anteriorly directed angle of incidence. In *Pterygoplichthys* this muscle also inserts upon lateropterygium; however, the effect of this insertion will not be discussed at present. Since this muscle spreads the fin and raises the anterior edge, the effect would be a raising of the caudal region.

The adductor superficialis (FIGURE 49, *Add. Sup.*) brings the fin postero-dorsally, concurrently folding it close to the body. This results in a decrease in the lift-area, or any resistance to forward motion caused by spread fins. The adductor profundus (*Add. Prof.*) rotates the whole fin dorso-posteriorly without opening or closing it. That is, it brings about a typical sweep of the fin that could be used in swimming or fanning activities. It tends to drop the tail region somewhat, since the pelvic fins are brought into an almost horizontal plane with the anterior, or entering edge, somewhat lower than the rest of the fin. All of these motions are used in stabilizing and turning. The functions are discussed in the historical review.

In the case of *Ameiurus nebulosus*, the peculiarity in the use of the fins which is of interest here is the vigorous fanning movement used in incubation. It seems unnecessary to explain this action minutely, since it is easily seen that it can be accomplished by various combinations of the pelvic muscles discussed above, the main power sweeps being those caused by contraction of the profundus muscles with the fin spread.

Pulley-arrangement

As we have seen before, the lateral process in *Plotosus arab* turns dorsally, inserts upon the lateral body-wall muscles, and forms a loop about the tendon of the arrector dorsalis (FIGURE 46); or more properly it might be said that the tendon of the arrector dorsalis is made to pass through an "eyelet" whose bottom border is formed by the basipterygium, the top border by the body-wall muscles, the lateral border by the ascending branch of the lateral process, and the medial border by the pelvic muscles. Thus, when the first ray has been drawn anteriorly by the arrector ventralis to such an extent, that the long axis of the first ray makes an angle with the long axis of the body greater than that made by the long axis of the arrector dorsalis when its tendon is pressed against the ascending section of the lateral process, the lateral process acts as a pulley, and instead of spreading the fin by drawing the first ray anteriorly, the direction of the force applied changes from one parallel to the long axis of the arrector dorsalis to one parallel to the long axis of the portion of tendon distal to lateral pro-

cess, and the first ray is moved toward the body. The contraction of the arrector dorsalis, however, will still draw the first ray dorsally. The functions of the other muscles are not changed.

In *Doras* a similar condition occurs. The main difference is that the lateral process enters into the body-wall muscles, rather than being attached to them superficially as is the case in *Plotosus*.

The different type of pulley-arrangement occurs in *Ageneiosus*, where the lateral motion of the tendon of the arrector dorsalis is limited by the fact that it has cut into the posterior edge of the lateral process, so that it moves in a notch in this process (FIGURE 39).

In *Xenocara*, still another form of pulley-arrangement is present, consisting in this case of a tendon, the lateral tendon of the lateropterygium (FIGURE 53, *L. T. Lpt.*), which extends from the medial side of the lateropterygium to the edge of the basal plate. The tendon of the dorsalis passes through the opening which is limited by the lateropterygium, basipterygium, and the lateral tendon of the former structure. Its lateral motion is thus limited.

Possible Uses of the Lateropterygium

In *Astroblepus* a possible function of the lateropterygium has been hypothesized, based upon the following observations: When the fin is closed and the first ray is parallel to the body, the lateropterygium lies at an angle of from ten to twenty degrees with the horizontal. When the fin-ray is rotated away from the plate, the distal portion of the lateropterygium moves dorsally, so that when the first ray makes an angle of from sixty to sixty-five degrees with the long axis of the body, the lateropterygium has rotated dorsally until it is now perpendicular to the basal plate. During this activity its base becomes wedged between the head of the first ray and the lateral process (FIGURE 25, *L. P.*), which serves for the insertion of the protractor ischii. When the lateropterygium is in this position it is impossible to move the ray further anteriorly, that is, it can no longer be rotated as when it is being spread by the arrector muscles. Thus, this process functions as a lock to prevent the anterior rotation of the spine of the pelvic fins past a certain point. The practical application of this mechanism is found or at least hypothesized in connection with the "walking" habits of this form. It is evident that the spines of the pelvic fins are important in preventing backward slipping of the organism in its terrestrial migrations. In this activity, it is essential that the fin has a posteriorly directed resisting angle. This means that the angle which the spine makes with the long axis must be less than ninety

degrees. The blocking action of the lateropterygium prevents anterior rotation of the spine past this angle. This function might be taken over by muscular tension of the pelvic muscles; however, this would require the utilization of large amounts of energy.

In the case of *Pterygoplichthys* is was noted that the myotomes inserted upon the lateropterygium both anteriorly and posteriorly. Also, the lateropterygium was attached distally to the body-armor by a tendon. Contraction of the anterior myotomes will, therefore, cause the lateropterygium to rotate ventrally about the point of attachment to the armor which point will act as a fulcrum. The effect of this action upon the pelvis will be to move it ventrally. The contraction of the posterior myotomes, on the other hand, will cause a dorsal rotation of the lateropterygium about the same fixed point. Concurrent with this action, there will be a dorsal movement of the pelvis. It is conceivable that the ventral motion of the pelvis, consequent on the contraction of the anterior myotomes, followed by a dorsal movement resulting from contraction of the posterior myotomes, might form a suction, the pelvis acting as a piston, while the rigid lateral and dorsal body-armor serves as a cylinder.

Variations Correlated with the Clasper-function

As was described previously, the sixth ray in the female specimen of *Hexanematichthys* is modified into a clasper-like structure (FIGURE 27, *C. R.*) whose exact function is unknown. Hardenberg (1935) shows that an homologous structure in *Arius maculatus* is used as a clasper in the spawning act. Breder assumes that the function may be the same in *Galeichthys*. This view is supported by the findings in the pelvic myology of this form (FIGURES 31 and 33). It was seen that the parts of the adductor superficialis, adductor profundus, and abductor profundus, which insert on this ray are separated as almost completely independent slips in the case of the first two muscles and a partially independent slip in the case of the last. Moreover, these slips, especially that slip of the adductor superficialis which is really an independent muscle (FIGURE 33, *Add. Sup.''*), are heavier and stronger than the remainder of the muscles from which they have separated. This differentiation of slips inserting on this ray to form almost independent muscles seem to be a clear indication of a powerful grasping function for this modified ray, possible as a clasper.

Variations Correlated with Walking Habits

The method which the walking catfishes *Astroblepus marmoratus*, *A. longifilis*, and *A. homodon* use in progressing over land have been

discussed in the review of the literature. The method which is of interest here is that in which the pelvic fins are the primary organs of locomotion. It will be recalled that the essential elements of this activity are a drawing forward of pelvis and pelvic fins by contraction of the protractor ischii while the body remains stationary, and a drawing forward of the body by a contraction of the retractor ischii while the pelvic fins act as a fixed point. The forms investigated are *Astroblepus* (*Cyclopium*) *homodon* and *Astroblepus longifilis.* The latter, though larger and therefore more easily studied, was less well preserved. Therefore, the study of the myology is specifically taken from *A. homodon* (FIGURES 57, 59, and 60), but the arrangement of muscles is the same for *A. longifilis.*

There are several modifications which expedite this type of locomotion in these forms. Considering the externals, it is evident that the presence of a strong, bony spine (FIGURE 59, *Sp.*) at the border of the fin will form a much better anchoring organ for the forward push than would a softer ray. Furthermore, the numerous small spinules (*Spl.*) on the spine will also prevent the fins from slipping on the subsurface because of increased friction when the body is shoved forward, while they will in no way hinder the forward slide of the pelvics when the latter are drawn forward by the protractor, because these spinules point toward the distal end of the spine. Internally, the locking effect of the lateropterygium on the fin-spines will prevent the spines from rotating to such a degree that their points will no longer dig into the interstices and irregularities of the subsurface, that is, there is no possibility of a posteriorly directed entering angle, but always a posteriorly directed resisting angle. Not only will the points be kept pointing in a posterior direction by this mechanism but they will be kept in this position without the expenditure of any energy by muscles. Still other modifications which facilitate these activities are found in the protractor (FIGURE 59, *P. I.*) and retractor ischii (FIGURES 59 and 60, *R. I.*). It will be recalled that, while in all other forms the main body of the retractor ischii inserts on or near the posterior part of the pelvis, in the case of *Astroblepus* it inserts on the anterior tip of the basal plate. This type of insertion makes possible a longer retractor ischii compared to the length of the body, than would a posterior insertion. Since the magnitude of the contraction of a muscle is proportional to its length, this type of insertion gives a greater length of contraction to this muscle, which in turn results in a greater motion of pelvis than will a posterior insertion. In addition, the anterior insertion will result in a rotating downward motion of fin spines

This is because there is a lever system in which the fulcrum is supplied by lateropterygium. Thus, the force applied at the anterior tip of the pelvis by the retractor ischii will cause a rotation of the pelvis about the point of attachment of the lateropterygia, since the latter will not "sink into" the body-wall muscles because of their large surface. The anterior end of the pelvis will move dorsally to some extent, while the posterior end of the plate and fin-spines will move ventrally. This will occur simultaneously with a forward thrust of the body by the retractor, and therefore will, by digging points of spines into the sub-surface, prevent a backward slip of the pelvic fins. The protractor ischii is also modified in this form, but the exact effect of these modifications is not clear. One change from the other form is that the protractor ischii is independent and distinctly separate from the remainder of the great ventral muscle along the whole length from the origin on the cleithrum to its insertion on the basal plate; this, of course, makes it independent in action from the body-wall muscles. If the protractor ischii were merely a slip of the great ventral, as it is in other forms, there might be difficulty in getting it to contract without simultaneous contraction of the posterior myotomes which would partially nullify its effect. A second variation is that the fibers of the muscle are spiraled; that is, the muscle has the appearance and structure of a twisted hemp rope. Just how this affects the physiology of the muscle is a moot question. It is conceivable that it increases the magnitude of contraction. In other words, a spiraled muscle may be able to contract a greater fraction of its length than a muscle whose fibers are straight. It seems probable, also, that when such a muscle contracts it would tend to twist the basipterygium; the effect of such a function will be observed below. The investigation of the properties of such a muscle should serve as a very interesting problem in muscle physiology; unfortunately, the author was unable to get any living material.

Johnson (1912) states,

> "It is evident that the fish [*Arges marmoratus*] is able to create a suction pressure in the region of plate [pelvis], though how this is accomplished is not apparent from the structure."

A possible explanation of this phenomenon is that when the first ray is extended laterally, the consequent upward rotation of the lateropterygium, discussed under "locking" effect of this structure, forces the pelvis ventrally like a piston. Subsequent folding of the fin and consequent drop of the lateropterygium, with a simultaneous contraction of both protractor and retractor ischii, would lift the pelvis and concurrently develop a ventral suction. Another explanation

might be found in the spiraled protractor ischii. The action would be as follows: upon contraction the protractor ischii, due to its spiraled fibers, rotates the two halves of the basal plate so that it would bend, the center becoming reaised. Such an action could develop a suction.

Variations Correlated with Perching Habits

Although it was impossible to obtain any specimen of *Otocinclus* for dissection, a specimen was examined externally. It is from external appearances, a form very similar to *Pterygoplichthys*, but is much smaller. The border-ray of the pelvic fin is modified into a strong spine bearing spinules which point toward the distal end of the fin as in the case of the *Astroblepus*, *Pterygoplichthys*, *Xenocara*, and other genera. This spine with its spinules would be a great aid in the habit of perching on the vertical stem of water-plants by grasping them with ventral fins. Since the externals in *Otocinclus* are so similar to those of *Pterygoplichthys*, it seems quite probable that the internal anatomy, including the anatomy of the pelvis, is very similar. If so, there are a number of factors which would aid their grasping function. They are as follows: first, the well-developed head-processes upon the first ray, which would provide a comparatively long lever-arm for the action of the abductor superficialis (this inserts on the ventral process of the first ray and, therefore, gives a considerable force to this action); second, the presence of a hemispheric articulating condyle for the first ray, which facilitates a medial and ventral rotation; third, decussation of the abductor profundus, which effectively increases the length of that muscle and therefore the magnitude of contraction, and consequently the magnitude of ventro-medial movement of the fin.

Variations Correlated with "Basket Formation"

The "basket formation" discussed in connection with the reproductive habits of *Corydoras* has a definite morphological correlation. In the first place, the arrector dorsalis in this form has shifted its main body from the dorsal to the ventral region (FIGURE 61). This means that both arrector muscles now draw the first ray ventro-medially. Another factor is the comparatively large angle formed by the two basiptergyia (FIGURE 26). The lateral edge of the pelvis thus points ventro-laterally rather than laterally, and so the plane of the fins, when they are under no stress from the pelvic muscles, is no longer horizontal, but is tipped ventrally from the horizontal. This brings the fins into a position where they can more readily form the basket and the shift of the arrector dorsalis supplies more muscles for the ventral traction necessary for "basket formation."

Variations Correlated with Life in Torrential Streams

As has been seen in the literature, Hora (1923) has found various changes in the morphological characteristics of the pelvic region which adapt *Glyptosternum, Glyptothorax,* and *Pseudecheneis* to their life in the rapid streams of the Khasi Hills. These are completely discussed in the review of the literature and they are pointed out here merely to show further that there is a definite correlation between pelvic morphological characteristics and vital habits and habitus.

Summation

In conclusion it may be said that wherever there are functional idiosyncrasies as described by Breder (1935) and other authors, morphological characteristics and variations can be found which will facilitate those activities. On the other hand, there are many structural variations with which no function can be correlated, due probably to the incompleteness of the literature on the life-habits of these forms.

EVOLUTION

Derivation of the Nematognath Pelvis from that of Lower Ostariophysi

In a study of the derivation of the nematognath pelvis from that of lower forms, *Amia* is the logical starting-point, since it is from this form that teleosts are derived, according to Macfarlane (1923) and others. However, in this discussion, *Polypterus* will serve as the starting-point.

In *Polypterus* (FIGURE 9), the two halves of the girdle are connected only at the anterior end by an independent cartilaginous piece (*A. C.*); at the posterior end, however, there is the beginning of a medially directed process, the processus medialis (*P. M.*). In *Amia* (FIGURE 10), the anterior connecting cartilage has disappeared. The number of radials has been reduced and they have become cartilaginous. In *Salmo* (FIGURE 11), the two processi mediales (*Proc. med.*) have grown so as to meet in the mid-line while the anterior ends are further separated and a flat plate is forming upon the medial side of the main rachis. Posteriorly, there is a pair of cartilaginous, rod-like posterior processes.

In *Cyprinus* (FIGURE 12), the posterior fusion of the two halves of the girdle is stronger, the plate is better developed, and the basiptery-

gium has bifurcated slightly anteriorly, giving rise to a processus medialis anterior (internal anterior process) and a processus lateralis anterior (external anterior process) analogous to the rachis of lower forms. There are pronounced ridges upon the pelvis for the origin of muscles. The posterior process (*Proc. Med. Post.*) in this form has become larger, and is an integral ossified part of the basipterygium.

The general changes in the derivation of the nematognath pelvis from that of *Cyprinus* is probably as follows: the bifurcation becomes deeper, the plate flattens and broadens, and the posterior connection between the two basipterygia increases in length anteriorly. A third anterior process is formed (FIGURE 13).

Within the nematognath group, the main changes occur in the anterior processes, lateral processes, and posterior processes, along with general modification in contours and myology of the pelvis. The evolutionary series in the case of each of these structures will be postulated and then a composite series will be formed, based upon the independent series.

Posterior Processes

The posterior process will be the first to be discussed. In *Plotosus* (FIGURE 21), and *Hexanematichthys* (FIGURE 19), there are no posterior processes. In *Ameiurus* (FIGURE 18), *Doras* (FIGURE 36), and *Rhamdia* (FIGURE 42), the posterior process (*P. P.*) is cartilaginous and rod·like, while in *Ageneiosus* (FIGURE 42), it is flat and cartila ginous. In all of these cases, except the last, the posterior process inserts directly into the retractor ischii. In *Ageneiosus*, it inserts after a fashion, since it passes between the two retractor muscles (*R. I.*, *R. I.'*), the second of which is a new derivative of the retractor ischii. In *Astroblepus* (FIGURE 25), the posterior processes are long, rod-like, and well ossified, except for the posterior cartilaginous tips, while in *Pterygoplichthys* (FIGURES 22 and 23), the posterior processes (*P. P.*) are ossified but flat. This condition is also characteristic of *Xenocara* (FIGURE 17) and *Farlowella* (FIGURE 55).

In *Corydoras* (FIGURE 26), the posterior process is lobate, flat, ossified, and lies in a plane somewhat dorsal to that of the fins.

It would seem at first glance that the most primitive condition is that found in *Hexanematichthys* and *Plotosus*, where there is no posterior process. However, since a well developed posterior process occurs in *Cyprinus* and other less specialized *Ostariophysi*, and also because it appears from the drawings made by Dr. Norman that this process is present in *Diplomystes*, which is without doubt the most

primitive of all the nematognaths, it is probable that *Plotosus* and *Hexanematichthys* represent a condition in which this structure is secondarily lost. It would be interesting to determine whether or not this process appears in some stage of the ontogenetic development of these forms.

The presence of a cartilaginous, rod-like posterior process in *Ameiurus*, *Doras*, and *Rhamdia*, may be interpreted in two ways. It may mean that the osseous posterior process in *Cyprinus*, and possibly in *Diplomystes*, has been replaced in higher forms by a cartilaginous structure. The origin of this suggestion, which implies the occurrence of a regressive evolution, that is, replacement of a bony structure by a cartilaginous one, has not been located in the literature. The source of this idea is in the work of Eric Stensiö, the paleontologist, and the hypothesis was made known to the present author during a discussion with W. K. Gregory. If this hypothesis is applied, *Hexanematichthys* and *Plotosus* will represent a secondary condition as far as the development of the pelvis is concerned. The other possibility is that in phylogenetic development *Hexanematichthys* and *Plotosus* represent an intermediate form between *Cyprinus* and *Diplomystes* and the higher nematognaths, such as *Xenocara* and *Astroblepus*, where there is a bony posterior process. The implication of this second theory is that the posterior process in lower forms atrophies and disappears in the course of the phylogenetic development, *Hexanematichthys* and *Plotosus* representing forms in which it is entirely absent. The cartilaginous posterior process of *Ameiurus* and other genera, by this theory, represents a new formation rather than a derivative of the more primitive bony structure. This does not necessarily mean that *Hexanematichthys* and *Plotosus* actually represent the forms from which the higher nematognaths were derived, but rather that they are offshoots of the central stem at a point where this condition was present. It seems less probable that evolutionary reduplication in such a limited and clearly defined group as the *Ostariophysi* should take place, than that there should occur replacement of bone by cartilage.

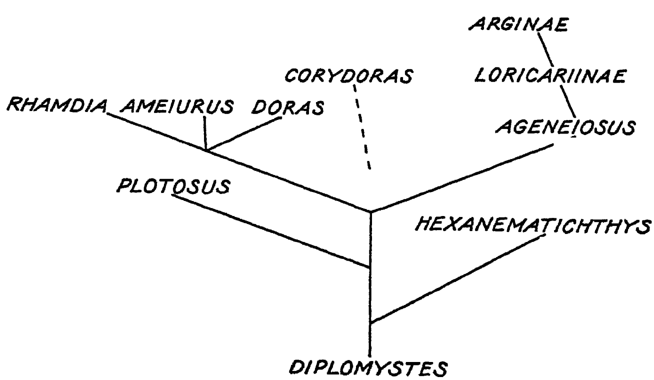
The flat, cartilaginous posterior processes are, of course, closely related to the rod-like, cartilaginous structures in *Ameiurus* and its allies. There is another difference, however. In the case of the rod-like processes, the proximal ends of the rods, where they are attached to the basipterygium, are raised as if they were rods which had been cemented upon the ventral surface of the pelvis. In the case of *Ageneiosis*, however, the posterior processes are perfectly continuous with the main body of the basipterygium, so that it is impossible to tell where the plate ends, and the posterior process begins.

In the *Arginae* (*Astroblepus*), the posterior processes are ossified but rod-like. It might appear that the pelvis of *Arginae* had been derived from the ameiurid type of pelvis with rod-like cartilaginous posterior process, while the type of pelvis characteristic of the *Loricariinae* had been developed out of the flat cartilaginous posterior process of the *Ageneiosinae*. There are several drawbacks to this theory. In the first place, it seems improbable that the highly characteristic lateropterygium, appearing in both *Arginae* and *Loricariinae* should be derived in two separate branches of the *Nematognathi* almost simultaneously. Furthermore, in both these latter forms the posterior process passes insensibly into the plate, thus indicating that both pelves are derived from the *Ageneiosinae* type. Since *Loricariinae* have a flat posterior process, it appears that they are closer to the *Ageneiosinae* than are the *Arginae* whose posterior processes are rod-like. The rod-like character in the latter group is apparently a secondary appearance of rod-like posterior processes and represents a stage that has passed through the flat osseous stage.

Another point in favor of this view is the fact that in all of the forms having a rod-like posterior process, this structure projects into the body of the retractor ischii so that the distal end of the cartilage is covered by the body of the muscle, and the muscle inserts, at least in part upon the distal end of the posterior process (FIGURES 29, 35, and 40). In *Ageneiosus*, on the other hand, the retractor ischii does not insert on the posterior process nor does the posterior process enter the body of this muscle. It lies ventral to the retractor ischii (FIGURE 39, *R. I.*), and the posterior part of protractor ischii (FIGURE 38, *R. I.'*) passes ventrally to the cartilaginous process. This latter fact causes it to appear that the retractor ischii inserts on the posterior process while in reality the latter lies between the produced protractor ischii and retractor ischii, without being inserted upon by either. The fact of this matter that favors the *Ageneiosinae-Loricariidae* bond is that in neither *Pterygoplichthys* (FIGURE 40), *Xenocara* (FIGURE 51), *Farlowella* (FIGURE 54), nor *Astroblepus* (FIGURE 59), does the distal end of the posterior process insert into the retractor ischii. Yet another fact which supports the hypothesis is that the border-ray of the pelvic fin in *Ageneiosus* is unbranched and thickened, though not stiffened to form a spine, while in all other forms except in the families *Loricariidae* and *Callichthyidae* it is undifferentiated, soft, and branched. In the *Loricariidae* the border-ray is modified to form a heavy stiffened spine. It may well be that the thickened and unbranched border-ray in *Ageneiosus* is the precursor of the border-spine in the *Loricariidae*.

In *Corydoras* the posterior process (FIGURES 26 and 62, *P. P.*) is ossified but, unlike the other forms with an ossified posterior process, there is an indication of a line of demarcation between the posterior processes and the main body of the basipterygium in the form of a ridge on the dorsal side of the posterior process. This would seem to indicate that the *Corydoras* girdle had been derived from the ameiurid type with rod-like discrete cartilaginous posterior process. However, the posterior process is so different in character that the above argument bears little weight. It is further contradicted by the fact that the border-ray is modified as a fairly well-developed spine, and also the fact that the retractor ischii does not insert on the posterior process, but rather upon a structure, the ventral process, that appears in none of the other forms. These latter characters, it will be recalled, belong to the *Ageneiosinae-Loricariidae* group. It thus seems that *Corydoras* is an anomaly in either of the above groups. This is probably due to the fact that it is a member of a highly specialized family and that the pelvis is highly modified in consequence of a functional idiosyncrasy. It is quite possible that the structure which has been designated as posterior process is not analogous to the structure of the same name in other forms. The posterior structure in other forms may correspond to the ventral process in *Corydoras*. The only evidence for this is the insertion of the retractor ischii on this latter structure. It is evident that the relationships of *Corydoras* must remain uncertain until the phylogeny of some of the other structures has been worked out.

Upon depicting the findings and interpretations regarding the posterior process of the basipterygium graphically, the resulting genetic tree is shown in DIAGRAM C:



C

Lateral Processes

In this investigation of the lateral process (*L. P.*) we again find that *Hexanematichthys* (*Galeichthys*) (FIGURE 19) presents a condition which is apparently primitive, that is, the absence of any kind of a lateral process. In this case, the forms which present a similar stage of complexity are *Diplomystes* (FIGURES 27 and 28) and *Ameiurus* (FIGURE 18). In *Rhamdia* there is a very rudimentary cartilaginous lateral process (*L. P.*) which passes laterally, then dorsally, and attaches to the lateral wall-muscles. In both of these forms the lateral process acts as a pulley-arrangement for the tendon of the arrector dorsalis, as was explained in the discussion of form and function. In *Ageneiosus* the lateral process is cartilaginous. It does not turn dorsally but extends laterally for its whole length. It has a pulley-action because the tendon of the arrector dorsalis has cut into it.

In the *Arginae* (FIGURE 25) we have two lateral structures to consider. First, the lateral process (*L. P.*) which is ossified and an integral fused part of the pelvis; and second, the lateropterygium (*Lpt.*) which is partly ossified and articulated to the pelvis. In the *Loricariinae* (FIGURES 22, 23, and 48–56) there is a well-developed lateropterygium as well as various processes (FIGURE 22, *L. P.*; FIGURE 52, *P. R. E. P.*) which might possibly be interpreted as lateral processes.

The evolution of the forms up to those where the lateropterygium is present is not very complicated. The primitive forms are *Diplomystes* (FIGURES 27 and 28), *Ameiurus* (FIGURES 18, 29, and 30), and *Hexanematichthys* (*Galeichthys*) (FIGURES 19 and 31–33), in which there is no lateral process. As has been seen from a study of the posterior process, *Hexanematichthys* may be considered as an aberrant offshoot from a primitive stem, and when it is also seen that it has no lateral process, we may assume that it came off the primitive stem before that process had developed. *Ameiurus* may, on both counts, that is, posterior process and lateral process, be placed as a direct offshoot of *Diplomystes* as far as pelvic girdle is concerned. The next higher stage of complexity occurs in *Rhamdia* (FIGURES 40, 41, and 42), where there is a rudimentary cartilaginous process which serves as the insertion of a special slip of the great ventral muscle which I have designated as the protractor lateralis (*P. L.*). In its next stage the lateral process takes on a new function, the pulley-action which has been discussed previously. There are three genera that show this complex, namely, *Plotosus*, *Doras*, and *Ageneiosus*. In the last the lateral process (*L. P.*) and its method of serving as a pulley-apparatus differ from those in the others in that the process does not turn dorsally

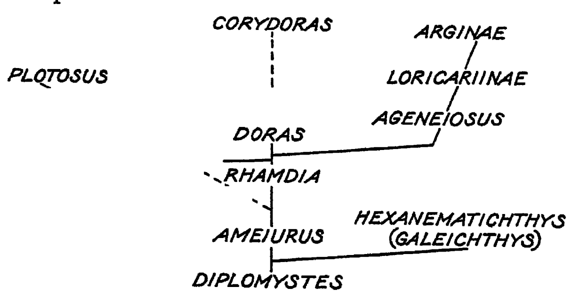
and, therefore, does not insert upon the lateral body-wall muscles. *Ageneiosus* is related to both *Rhamdia* and *Doras* by the presence of a protractor lateralis which inserts upon the lateral process. In *Plotosus*, on the other hand, there is no such muscle inserted on the lateral process, although this latter inserts upon the lateral body-wall muscles. The relationships are, so far, as follows: *Rhamdia* has the simplest type of lateral process, one that is small and neither bends dorsally to insert on body-wall muscles nor acts as a pulley-apparatus by limiting lateral motion of the tendon of the arrector dorsalis and anterior motion, or rotation, of first ray. From this form, the lateral process of *Doras* is derived by increase in size and growth in a dorsal direction with insertion on lateral body-wall muscles and consequent pulley-action, and also by the differentiation of the sub-protractor lateralis. *Plotosus* is derived from the *Rhamdia* type in a similar manner, but, in addition, the insertion of the protractor lateralis is lost. *Ageneiosus* type is derived from the *Rhamdia* type by a lateral growth of the lateral process and a cutting into this process by the tendon of the arrector dorsalis. These three forms are, therefore, all offshoots of the *Rhamdia* type, and *Plotosus* is aberrant or regressive in its loss of insertion of the protractor lateralis.

The derivation of the higher forms, *Corydoras*, *Astroblepus*, and the armored *Loricariidae*, is not so simple. It would seem that the lateral process of *Corydoras* develops from the plotosid stem since there is no protractor lateralis inserted on it. In the case of the armored *Loricariidae* the main problem is to determine just what represents the lateral process of lower forms. In *Pterygoplichthys* (FIGURES 48–50), there is no protractor lateralis separated from the great ventral muscle. However, the lateral body-wall muscles do insert on the lateropterygium. This seems to favor the view that this latter structure is analogous to the lateral process of lower forms, but whether this insertion of lateral body-wall muscles represents a derivation from the insertion of the protractor lateralis and lateral body-wall muscles of *Doras* or *Plotosus*, or the insertion of the protractor lateralis of *Ageneiosus*, is a moot question. However, if some of the findings concerning the posterior process and the border-ray are used to straighten out the matter, the logical conclusion is that the *Ageneiosus*-stem is the proper point of origin for the loricariid group. A possible mechanism for the derivation of the lateropterygium from a lateral process similar to that of *Ageneiosus* has its basis in the fact that the tendon of the arrector dorsalis in this latter form, as discussed previously, has cut into the lateral process to some extent. It is conceivable that the

cutting could continue to such an extent that the distal portion of the lateral process is completely separated from the basipterygium. This separate piece may then give rise to the lateropterygium. If the lateral process were cut off in an ancestral form, it could not be transmitted as a separate process to the progeny of this ancestor inasmuch as acquired characteristics are probably not transmissible. However, the propensity to the cutting off of this process may be transmitted, and in these higher forms, the actual separation may take place in the ontogenetic development. The problem of whether or not such a phenomenon takes place in the embryonic development is one that might well be investigated by an embryologist who has the materials necessary on hand. A feature of these forms (*Loricariinae*) is the point of insertion of the protractor ischii (*P. I.*). In *Pterygoplichthys* (FIGURE 48) this muscle inserts all around the edge (ventral ridge) of the external process. *Xenocara* has the same general arrangement, but two heavy strands of muscle (FIGURE 51, *P. I.* and *P. I.'*) are differentiated from the main body of the muscle and insert on projections (*P. R. E. P.*, *P. R. I. P.*) of the ridges of the external and internal processes. In *Farlowella* (FIGURE 54) the protractor has become narrower and shifted over to the most latero-posterior part of the ridge of the external process. The insertion of the protractor ischii will be important in determining the homologies in *Astroblepus*.

In *Astroblepus* the protractor ischii (FIGURE 59, *P. I.*) is inserted upon a laterally-directed, ossified, lateral process (FIGURE 25, *L. P.*). This might well represent the cartilaginous lateral process of lower forms. However, there can be no doubt that the flat, disc-like lateropterygium of *Astroblepus* is analogous to the rod-like structure of the same name in the armored loricariids, and since in these latter forms there is no process that can very well be homologized with the lateral process of lower forms except the lateropterygium, it is possible to assume that the lateropterygium of *Astroblepus* is analogous to the cartilaginous lateral process of lower forms. This leaves the bony lateral process (*L. P.*) in *Astroblepus* without homology. Some light is shed on this problem by the migration of the protractor ischii in the other forms studied. In all of the lower forms except *Ageneiosus* the protractor is inserted on the posterior process or the posterior border of the basipterygium. In *Pterygoplichthys* it has migrated anteriorly and inserts on the ridge of the internal process. The next higher stage is that found in *Xenocara*, where thickened strips of muscle appear in the protractor ischii and insert on special projections on the ridge of the internal process, one of which (*P. R. E. P.*) is near the

lateral border of the basipterygium. In *Farlowella* the only part of the protractor persisting is the part which inserts on the most laterally situated process of the ridge of the internal process mentioned above, and even this point of insertion has shifted farther laterally. It may, then, be assumed that *Astroblepus* presents the end-product in this lateral migration of the point of insertion of the protractor ischii, and that the lateral bony process (*L. P.*) in *Astroblepus* has taken the place of the projection of the ridge of the internal process in *Xenocara* and *Farlowella*, though it is not necessarily derivative of the latter. Since it has been assumed that the lateropterygium in the armored loricariids is a derivative of the cartilaginous lateral process of lower forms, and since it has further been assumed that the lateropterygium in *Astroblepus* is a derivative of that in the armored loricariids, it is necessary to assume that lack of any muscle-insertion upon this structure in the former genus is a secondary loss of such insertions. It is of interest to note that in *Xenocara* there is a reappearance of a pulley-arrangement in connection with the lateral process, the lateropterygium in this case. The pulley-arrangement is unlike the types already discussed. The complex through which the tendon of the arrector dorsalis passes, and which limits the lateral motion of this tendon, is formed by a tendon (FIGURE 53, *L. T. Lpt.*) which stretches from the inner side of the lateropterygium to the dorsal surface of the pelvis near its lateral border, thus completing a triangular passage whose other two sides are formed by the lateropterygium and the basipterygium, and through which the tendon of the arrector dorsalis passes.



D. LATERAL PROCESSES

Corydoras again forms a stumbling-block. Its lobate osseous lateral process serves for no muscle-insertion, but it does have a tendon (*L. T.*) which inserts on the body-armor. This might possibly, but not very probably, denote the fact that the lateral process in *Corydoras* was a derivative of the lateropterygium in the armored loricar-

iids, since this latter is also connected distally to the body-armor by a tendon. However, it seems better at this stage to assume that the evolutionary position of *Corydoras* is not very well defined either by its posterior or its lateral processes.

Graphical representation of the preceding conclusions based on structure and function of lateral processes results in the phylogenetic tree appearing as DIAGRAM D.

Anterior Processes

The final step, in the working out of the possible evolution of the pelvis within the *Nematognathi*, is the investigation of the stages in the structures and relationships of the anterior processes of the basipterygium.

Hexanematichthys (FIGURE 19) has two pairs of anterior processes. The internal ones (*I. P.*) are absolutely independent along their whole length. In *Diplomystes* (FIGURES 27 and 28) there are two sets of anterior processes (*E. P.* and *I. P.*) which are well developed. The medial ones approach each other much more closely than do those in *Hexanematichthys*. In addition there are two ridges (*Pt. M.*) on the ventral surface which are produced as extremely rudimentary processes. It will be recalled that in Sewertzoff's figures of an immature *Silurus glanis* (FIGURE 13) there is a third pair of anterior processes (*Pt M.*), which occupy an extreme medial position. *Ameiurus* (FIGURE 18) presents a pelvis with two pairs of rod-like anterior processes, those of the most medial pair (*I. P.*) being united across the midline by a cartilaginous connecting tissue (not shown in the drawing). A similar condition is found in *Doras*, *Rhamdia*, *Plotosus*, and *Ageneiosus*. In *Pterygoplichthys* these two anterior processes form a median triangular projection which has a foramen in the center, a pair of ridges along its border, and its two halves united in the midline by a cartilaginous connecting tissue. *Farlowella* is the same, except that the anterior processes are much shorter, and the median triangular part is also smaller. In *Xenocara* (FIGURE 24) there are two lateral foramina in the anterior part of the plate and a median foramen in the mid-line further posteriorly. *Astroblepus* has one pair of anterior processes and a median triangular area with no foramina. In *Corydoras* there are no anterior processes, but merely an extension of the body of the plate anteriorly from the region of the lateral process.

The apparent evolution of these forms is somewhat as follows:—*Diplomystes* represents a primitive form in which there remains the vestige of a third anterior process, which appears in the ontogenetic

development of *Silurus glanis*. In all of the forms higher than *Diplomystes* this third anterior process has disappeared altogether. The evolutionary process is, therefore, a concrescence of the third anterior process with the body of the plate. *Hexanematichthys* represents, in this case, as well as in regard to posterior process, an anomaly. The lack of proximation of the tips of internal processes seems to be a primitive condition derived from the pelvic structure in *Cyprinus* (FIGURE 12), in which the formation of two sets of anterior processes begins by a bifurction of the basal plate, and in which the medial branches of the bifurcation do not approach each other. Thus, it would appear that *Hexanematichthys* is more primitive in this respect than *Diplomystes*. The condition must be interpreted as a secondary offshoot which, however, represents a stage in the evolution of the higher pelves. In *Ameiurus, Plotosus, Rhamdia, Doras*, and *Ageneiosus*, we have a stage which is a resultant of two processes, viz., the disappearance of the third anterior process as evidenced by the appearance of that process in young *Silurus* and in *Diplomystes*, and the proximation of the tips of the internal processes, from a condition similar to that found in *Hexanematichthys*. Another stage appears in *Pterygoplichthys*. The assumption, in this case, is that the median triangular area represents the product of the fusion in the mid-line of the medial edges of the internal processes along a good portion of their length. The median foramen, it is assumed, is a remnant of the space between the internal processes of lower forms. Another factor which favors this view is the presence of ridges parallel with the edge of this triangular area, which ridges may represent ridges of original internal processes. A closely related condition is that found in *Astroblepus*, where the fusion of the internal processes along their medial edge is so complete that there is no evidence of the fusion, in the form of a foramen, left in the median area, and external processes are approaching each other anteriorly.

Another phase of the development is found in *Xenocara* (FIGURE 24), where the median part of the anterior region of the plate represents a fusion of the internal processes, with the median foramen representing the remainder of the space between the internal processes in lower forms, as in the case of *Pterygoplichthys*. The isthmus between the lateral foramina, it is assumed, represents the anterior part of fused internal processes. The bony strips forming the outer border of the lateral foramina represent the external anterior processes which have turned medially, and had their tips fused to the remainder of the internal processes. The lateral foramina are, therefore, the remnants

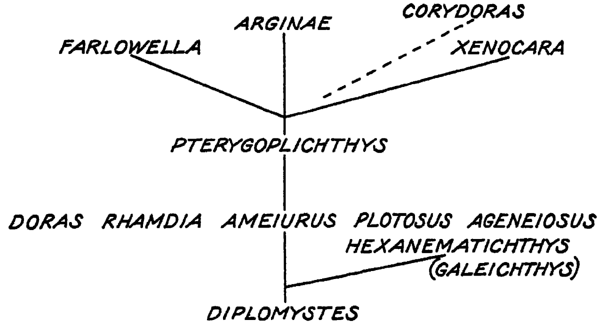
of the space between the internal and external processes in lower forms. This hypothesis is substantiated by the presence of two pairs of ridges (*E. P.* and *I. P.*), one anterior and the other posterior to the lateral foramina, representing the ridges of external and internal anterior processes of lower forms.

Farlowella (FIGURE 55) represents a form in which the internal processes have fused, but in which the external processes are combined, not by turning medially and fusing with central elements, but by having the plate grow out between external and internal processes.

Corydoras (FIGURE 26) may represent the end-product of the concentration process that has been followed through the other forms, the single median anterior projection representing the product of combined fusion of both internal and external processes; that is to say, a closing up of foramina in *Xenocara*. The presence of a specialized border-ray also places *Corydoras* as an offshoot of the *Ageneiosinae-Loricariidae* stem.

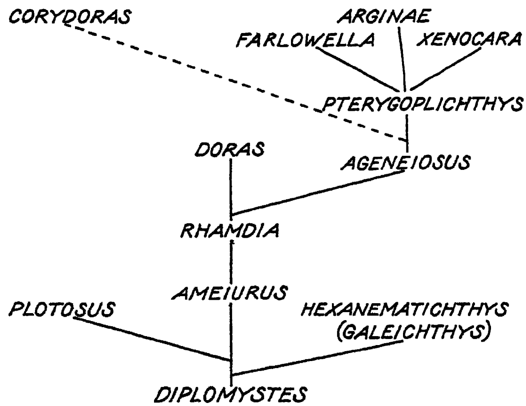
A summary of this process is as follows: In the first stage there are three sets of anterior processes, in the course of events the most medial combines with the basal plate, which process is either followed or accompanied by a medial bending of the internal processes of the basipterygium, which first become connected by a tendon across the midline, and later fuse in this region. The external processes next combine with a fused internal process, either by the medial bending and fusion at tips of external processes, as is illustrated in *Xenocara*, or by an outgrowth of the plate into the region between the external and internal processes, as is illustrated in *Farlowella*. The end-product is a complete concrescence of both pairs of anterior processes.

When these findings are depicted graphically, the resulting phylogenetic tree is shown in DIAGRAM E:



E. ANTERIOR PROCESSES

Examination of the three series worked out upon the pelvic structures in the preceding pages shows that each series differentiates most highly in a different region. By combining these three, a general representation of the relative complexity and relationships of the various pelves may be obtained. DIAGRAM F is an example of such a combined series:



F

Myology in Evolution

It may seem strange that after spending considerable time and space in the consideration of the nematognath pelvic myology, the musculature has not been used, per se, in the postulation of the evolutionary series. So far, the observations in this field have been used only in the determination of homologies of various parts of the bony structure, and to illustrate anatomical variations correlated with various peculiar functions. There are reasons for this. In the first place, the method and state of preservation have a much more marked effect upon muscles than upon bony structures, and since all the forms studied were preserved, it is probable that the bony structure is more nearly like that in the living animal than is the musculature. Then too, there are so many small and minor variations in the muscles that it is hard to determine which ones are the significant ones. A short discussion of the main variations in the musculature follows, and from this it will be evident what are the possible steps in the evolution of the muscle-structures.

Ameiurus represents the simplest arrangement investigated. It has the general complement of six purely pelvic muscles, but the arrector ventralis is only partially separated from the abductor super-

ficialis. Both retractor and protractor ischii are inserted on the posterior process.

Hexanematichthys represents a form which is rather highly specialized. The adductor superficialis is divided into three slips, the part of the adductor profundus which inserts on the clasper-ray is more or less independent from the rest of the muscle, and the abductor superficialis is also divided into two parts. All of the muscles are exceptionally heavy. The retractor ischii inserts upon the posterior end of the plate, since there are no posterior processes.

In *Plotosus* the purely pelvic muscles are well developed and generalized in character. As in *Hexanematichthys* the retractor ischii inserts upon the posterior end of the plate. The protractor ischii inserts in the mid-line at the posterior end of the plate.

In *Rhamdia* we have the same condition as in *Ameiurus,* but the arrector ventralis is completely separated from the abductor superficialis, and the protractor lateralis has been differentiated from the great ventral muscle.

Doras is almost the exact counterpart of *Rhamdia,* but the subprotractor lateralis has been developed.

Ageneiosus is a rather aberrant form. The protractor ischii is produced posteriorly to insert on the basal element of the anal fin, the arrector ventralis is a large fan-shaped muscle, and the protractor lateralis, originating as it does from beneath the protractor ischii rather than beside it, is apparently the analogue of the subprotractor lateralis in *Doras.*

Pterygoplichthys has the usual complement of six pelvic muscles. However, the adductor superficialis is narrower than usual, and inserts only upon the first ray. There is decussation of the abductor profundus, and the insertion of the protractor ischii has shifted anteriorly to the ridge of the internal process.

Xenocara is very similar, but a special slip of the retractor ischii is differentiated which inserts upon the lateropterygium. Two bands of muscle within the protractor ischii have become heavier than the remainder of the muscle, and insert on special projections of the ridge of the internal process.

In *Farlowella* the only difference from *Pterygoplichthys* is that the protractor ischii is smaller, and inserts only upon the postero-lateral end of the ridge of the internal process.

Astroblepus has the retractor ischii inserting on the anterior tip of the basal plate, and the protractor ischii is an independent muscle

rather than a slip of the great ventral muscle. There are two small independent muscles derived from the adductor profundus, and the abductor profundus has become very small.

Corydoras is quite normal, but there is no protractor lateralis, the abductor superficialis inserts only upon first two rays, and the arrector dorsalis has shifted to the ventral side of the basipterygium.

SUMMARY

The osteology and myology of twelve species of nematognaths, members of a fairly representative selection of families, were studied.

Osteology

It was determined that the "os pelvis" of the nematognaths consisted of two flat bony halves, the basipterygia, united in the mid-line either directly or through the mediacy of a cartilaginous middle piece. From the anterior end of the pelvis there may arise rod-like processes, varying in number in the different species. In some forms above the *Ameiuridae* there is a lateral cartilaginous extension of the basipterygium, the lateral process. The loricariid girdle has an articulated rod-shaped piece, the lateropterygium. In the *Arginae*, the counterpart of this structure is thin and disk-shaped. From the posterior edge of the basipterygium of all genera except *Hexanematichthys* and *Plotosus*, there extend posteriorly a pair of projections, the posterior processes. In lower forms they are cartilaginous, while in the *Loricariidae* and *Callichthyidae* they are ossified.

Myology

The generalized musculature of the nematognath pelvis comprises six muscles upon each basipterygium. They are the arrector ventralis, arrector dorsalis, abductor profundus, abductor superficialis, adductor profundus, and adductor superficialis.

The protractor ischii, a slip of the great ventral muscle, inserts upon the posterior processes in lower forms, and more anterior regions in others. Another slip of the great ventral muscle, the protractor lateralis, often inserts upon the lateral process.

The retractor ischii is a muscle which originates altogether, or in part, upon the basal element of the anal fin, and inserts upon the posterior processes or posterior edge of the basal plate.

Any one or all of these muscles may become modified in various ways.

Correlation of Form and Function

The normal functions of muscles were determined by exerting an experimental traction upon the muscles, and observing the effect upon the fin. The results were as follows:—

The arrector ventralis draws the first ray ventro-laterally, and spreads the fin.

The arrector dorsalis has the same function but draws the ray dorso-laterally.

The abductor superficialis abducts the fin, and simultaneously folds the fin, bringing it close to the body.

The adductor superficialis has the same function as the preceding muscle, except that it adducts.

The abductor profundus abducts the fin, without either folding or spreading it.

The adductor profundus adducts the fin without folding or spreading it.

The retractor ischii draws the pelvis posteriorly, where the pelvis is movable.

The protractor ischii draws the pelvis anteriorly.

Morphological variations were found in each case mentioned by Breder (135) as having peculiar functions which would facilitate these functional peculiarities.

In the case of the clasper-ray of *Hexanematichthys* there are formed special heavy independent muscle-slips which insert upon it. In *Corydoras* the arrector dorsalis has shifted from the dorsal to the ventral side of the basipterygium to facilitate "basket formation." The retractor ischii of *Astroblepus* inserts on the anterior tip of the pelvis, rather than on the posterior processes, or the posterior edge of the basipterygium, as in the case of other forms. The protractor ischii is an independent muscle, rather than a slip of the great ventral muscle, and the fibers are spiraled. The lateroptergyium exerts a locking effect on the first ray, and prevents its rotating too far forward. All of these variations expedite the walking activities.

The perching habits of *Otocinclus* are favored by its small size and the general characteristics of the loricariid pelvis.

Evolution

The nematognath pelvis may be derived from that of the lower *Ostariophysi* or more specifically from that of *Cyprinus*, by a pronounced increase in the bifurcation of the basipterygium, atrophy of

radials, and broadening of medial connection between the two halves of the plate.

The main phases of the development are a concrescence of the anterior processes, so that beginning with the first stage with three pairs of these processes, the end stage has a single median projection. The second phase is the development of a lateral process, which is not present in lower forms, and gives rise to an articulated lateropterygium in the *Loricariidae.* The third phase is the development of the posterior processes from a rod-like cartilaginous stage through flat cartilaginous and flat ossified to rod-like and lobate ossified stages. The homologies of the various osteological structures are clarified by the myology in several cases.

QUESTIONS RAISED DURING THE INVESTIGATION

A number of questions, which can not be answered at the present time, have arisen during the course of these investigations. Some of these questions are:—

(1) What are the physiological properties of the spiraled muscle found in *Astroblepus homodon?*

(2) Does the lateropterygium develop ontogenetically by the cutting off of the distal portion of a lateral process by the tendon of the arrector dorsalis?

(3) Does a posterior process appear during any stage in the embryonic development of *Hexanematichthys* or *Plotosus?*

(4) Should the *Ariidae* be considered as primitive, as suggested by Regan's (1911) classification?

(5) What are the functions of the lateropterygium in the *Loricariinae?*

BIBLIOGRAPHY

Boulenger, George Albert.

1904. Teleostei (systematic part). Cambridge Natural History 7: 541–727.

Breder, Charles Marcus.

1926. The locomotion of fishes. Zoologica (N. Y.) 4: 159–297.

1935. The reproductive habits of the common catfish, Ameiurus nebulosus (Le Sueur), with a discussion of their significance in ontogeny and phylogeny. Zoologica (N. Y.) 19: 143–185.

Bridge, Thomas William; & Haddon, Alfred Cort.

1893. Contributions to the anatomy of fishes.—II. The air-bladder and Weberian ossicles in the siluroid fishes. Phil. Trans. Roy. Soc. 184 (B): 65–333. *pl. 11–19.*

Carbonnier, Pierre.

1881. Sur le Callichthys fasciatus Cuvier. Bull. Soc. Zool. France 5: 288–290.

Carlisle, Anthony.

1805. The Croonian lecture on muscular motion. Phil. Trans. Roy. Soc. 1805: 1–30.

1806. The Croonian lecture on the arrangement and mechanical action of the muscles of fishes. Phil. Trans. Roy. Soc. 1806: 1–12. *pl. 1.*

Carter, George Stuart; & Beadle, Leonard Clayton.

1931. The fauna of the swamps of the Paraguayan Chaco in relation to its environment.—II. Respiratory adaptations in the fishes. Jour. Linn. Soc. Zool. 37: 327–368. *pl. 19–23.*

Davidoff, M. von.

1880. Ueber das Skelett der hinteren Gliedmasse der Ganoidei Holostei und der physostomen Knochenfische. Morph. Jahrb. 6: 125–128.

Derjugin, Konstantin Mikhailovicz; Grieb, Alexander Benediktovicz; & Trifonowa, Anna Nikolaevna.

1934. Ueber die Homodynamie der Elemente des vorderen und des hinteren Gurtels sowie der Extremitäten bei den Teleostien. Anat. Anz. 78: 166–174.

Dugès, Alfred Auguste Delsescautz.

1905. Rôle des nageoires chez les Poissons. Bull. Soc. Zool. France 30: 107–110.

Eigenmann, Carl H; & Eigenmann, Rosa (Smith).

1890. A revision of the South American Nematognathi or cat-fishes. Occas. Papers Calif. Acad. Sci. 1: 1–508.

Evermann, Barton Warren; & Kendall, William Converse.

1905. An interesting species of fish from the high Andes of central Ecuador. Proc. Biol. Soc. Wash. 18: 91–105.

Fowler, Henry Weed.

1917. Some notes on the breeding habits of local catfishes. Copeia 1917: 32–36. *pl.*

Goodrich, Edwin Stephen.

1930. Studies on the structure & development of vertebrates. 1–837.

Gregory, William King.

1933. Fish skulls: a study of the evolution of natural mechanisms. Trans. Am. Phil. Soc. II. 23: 75–481.

Grenholm, Åke.

1923. Studien über die Flossenmuskulatur der Teliostier. 1–296. (Inauguraldissertation.) "Sonderabdruck aus: Uppsala Universitets Arsskrift 1923."

Günther, Albert Carl Ludwig Gotthilf.

1880. An introduction to the study of fishes. 1–720. *pl.*

Hancock, John.

1829. Fishes that travel on the land.—Doras costata, or hassar. Edinb. New Phil. Jour. 6: 396, 397.

Hardenberg, Johann Dietrich Franz.

1935. On the propagation of Arius maculatus (Thunb.). Natuurk. Tijdschr. Ned.-Indie 95: 54–57.

Hora, Sunder Lal.

1922. Structural modifications in the fish of mountain torrents. Rec. Indian Mus. 24: 31–61.

1923. Notes on fishes in the Indian Museum. V.—On the composite genus Glyptosternon McClelland. Rec. Indian Mus. 25: 1–44. *pl. 1–4.*

1927. Animal life in torrential streams. Jour. Bombay Nat. Hist. Soc. 32: 111–126. *pl.*

Innes, William Thornton.

1935. Exotic aquarium fishes. 1–463.

Johnson, Reno De O.

1912. Notes on the habits of a climbing catfish (Arges marmoratus) from the republic of Colombia. Ann. N. Y. Acad. Sci. 22: 327–333.

Jordan, David Starr.

1905. A guide to the study of fishes. 1: 1–624. 2: 1–599.

1923. A classification of fishes, including families and genera as far as known. Stanford Univ. Publ. Biol. Sci. 3: 77–254.

Koltzoff, Nikolai Konstantinovicz.

1896. Das primäre Skelet der Bauchflossen der Teliostier. Bull. Soc. Nat. Moscou II. 9: 514–522.

Leege, C. O.

1922. Der Rumpfpanzer der Panzerwelse und seine Skelettbeziehungen. Jenaische Zeitschr. 58: 145–270. *pl. 9, 10.*

Macfarlane, John Muirhead.

1923. The evolution and distribution of fishes. 1–564.

McMurrich, James Playfair.

1884. The osteology of Amiurus catus (L.) Gill. Proc. Canad. Inst. III. 2: 270–310.

1884. The myology of Amiurus catus (L.) Gill. Proc. Canad. Inst. III. 2: 311–351.

Nichols, John Treadwell.

1930. Speculation on the history of the Ostariophysi. Copeia 1930: 148–151.

Nichols, John Treadwell; & Breder, Charles Marcus.

1928. An annotated list of the Synentognathi, with remarks on their development and relationships. Zoologica (N. Y.) 8: 423–448.

Osburn, Raymond Carroll.

1907. The uses of the fins of fishes. Zool. Soc. Bull. N. Y. 2(25): 347, 348.

Rautenfeld, Eberhard von.

1882. Morphologische Untersuchungen über das Skelet der hinteren Gliedmassen von Ganoiden und Teliostiern. 1–47. *pl. 1, 2.* (Dissertation, Dorpat.)

Regan, Charles Tate.

1911. The classification of the Teleostean fishes of the order Ostariophysi.—2. Siluroidea. Ann. & Mag. Nat. Hist. VIII. 8: 553–577.

Schomburgk, Moritz Richard.

1848. [Lebensart des Callichthys coelatus.] In his: Reisen in Britisch-Guiana in den Jahren 1840–1844. 2: 411, 412.

Sewertzoff, Alexei Nikolaevicz.

1934. Evolution der Bauchflossen der Fische. Zool. Jahrb. Abt. Anat. 58: 415–500.

Smith, Hugh McCormick.

1903. Breeding habits of the yellow catfish (Ameiurus nebulosus). Science II. 17: 243, 244. [Abstract.]

INDEX

Annals of the New York Academy of Sciences
Volume XXXVII, pages 97–162, plates I–VI
April, 1938

STUDIES OF CERTAIN SOCIOLOGICAL AND PHYSIOLOGICAL FEATURES IN THE FORMICIDAE*

By
Caryl Parker Haskins
and
Ernst Vincenz Enzmann

CONTENTS

* Publication made possible through a grant from the income of the Ralph Winfred Tower Memorial Fund.

INTRODUCTORY NOTE

It has been the purpose of the work described in the following papers to reinvestigate, it is hoped in part from a new viewpoint, the questions of the power to perceive sound-vibrations aerially transmitted as it exists in the *Formicidae*, and the power to form independent colonies from isolated females as it exists in Ponerine ants. Both of these problems present important physiological aspects, which are of significance in studies both of phylogeny and of ethology of ants in general. A considerable volume of material has been published in the former field, much of it of great value, but the surprisingly conflicting results and conclusions obtained even by the best investigators have led the writers to attempt a completely new investigation, in an attempt to add to that background of evidence which at some future time may lead a qualified and fortunate worker in the solution of a difficult problem. Little appears to be known of the method generally adopted among Ponerine ants in the formation of new communities. The question would seem an important one in a study of the origin of communal life among the *Formicidae*, because of the extreme primitiveness of the group. Observations, collected over a considerable period of years, are presented. A study, which is presented herewith, has likewise been made of the degeneration of wing-musculature in the fertile Ponerine female—a physiological feature of considerable significance, not only because of its essential invariance in higher ants, but because of the important role which it plays in the higher types of Formicid social organizations. A more complete study of the same question, which is planned, may well have some significance in determining the line of descent of the true ants.

The writers would like to express their gratitude to Dr. W. M. Wheeler and Dr. Thomas Barbour, of Harvard University, for permission to stay at the Barro Colorado Island Biological Laboratory in 1930, 1931, 1932, 1933, 1934, 1935, and 1936 for the purpose of studying the habits of stridulation and of colony-formation in tropical *Ponerinae* and *Myrmicinae;* to Dr. James Zetek for his unfailing kindness and assistance; to Dr. E. R. Sasscer for permission to import tropical ants to the United States in living condition for further laboratory study; to Dr. R. D. Glasgow, the State Entomologist of New York, for his great kindness in placing at our disposal the literary and experimental facilities of his office; to Dr. A. T. Waterman of the Physics Department of Yale University for his interest and sugges-

tions; to Dr. E. B. Kelsey and Mr. Eugene Marchand of the Chemistry Department of Yale University in kindly arranging the setting aside of a room for the conducting of tests on living subjects; and, for their interest and general assistance, to Dr. G. W. Pearce, head of the Cruft Physics Laboratory of Harvard University, and Dr. C. T. Brues of the Biological Laboratory at Harvard. We have also been greatly helped by the generosity of Dr. Marion R. Smith, formerly of the State Plant Board of Mississippi, and Dr. Neal A. Weber, of the University of North Dakota, in supplying us with living material of *Euponera gilva harnedi*, *Proceratium croceum*, *Pseudoponera haskinsi*, and other semitropical and tropical Ponerine forms, which has made it possible to include representatives of important and little-known tribes in both physiological and psychological study.

PART I

PERCEPTION OF SOUND AND SOUND PRODUCTION IN CERTAIN ANTS

Historical Review

The extraordinary and rather apparent powers of "hearing," or, more strictly speaking, of the perception of and reaction to aerial vibrations within the human range of audibility, possessed by various Orthopteroid insects, early led investigators to consider the extension of this power in higher orders. Attention was further focused upon the problem following the discovery of von Siebold in 1844 of the chordontal organs, and the investigations of the organs of stridulation in *Orthoptera* and *Coleoptera*. It is not surprising that interest in the auditory powers of insects should have been extended particularly to social types, especially because of the intricate manner in which such a power might readily be employed, in conjunction with means of sound-production, in maintaining the integrity of a society. As early as 1810 Pierre Huber, in his remarkable work *Recherches sur les moeurs des Fourmis indigènes*, investigated this field, failed to obtain response in his ants to the sounds to which he subjected them, and concluded that the power of perception of aerial vibrations, seemingly well developed in lower orders, had not persisted in the highest insofar as it was represented by the *Formicidae.*

Since the time of Huber, a host of investigators have entered the field, including the most eminent known to myrmecology: Forel, Emery, Wheeler, Landois, Lubbock, Janet, Turner, Miss Fielde, Parker, Metcalf, Weir, Weld, Miss Wagner, and others.

Huber (1810) and Forel (1888), on the basis of rather exhaustive experiments in which the ever-present danger of the confusion of sound-vibrations with mechanical shock was rather carefully avoided, failed to obtain responses of any sort with living subjects, and both maintained the complete "deafness" of ants, even to vibrations above the humanly audible range. Lubbock (1882) repeatedly failed to obtain reactions, using a considerable number of sound-producing instruments of fork and reed types with a wide variety of species. His conclusion of deafness to sonant vibrations in those insects was tentatively established. Sounds above the audible range, he continued to believe, might well be perceived. Landois (1874a), on the contrary, came to the conclusion that ants are very definitely pos-

sessed of a sense of "hearing," but his evidence is questionable, since it seems almost certain that the confusion of mechanical shock vitiated his results. In all probability, too, Landois was influenced by his own discovery of a stridulatory organ in "*Ponera quadridentata.*"

More recent investigators have differed quite as widely in their opinions. Weir (1898), conducting a study principally concerned with Formicine ants, could obtain no responses whatever to sounds of ordinary pitch. When a fine hair-like wire, tautly stretched between two pegs on a wooden table and giving, according to Weir's statement, over 60,000 vibrations per second when struck, was sounded, a worker of *Lasius niger* resting on the same table reacted violently. Weir believed that this reaction was due to the perception of sound-waves aerially rather than mechanically transmitted, since a banjo string similarly placed and struck produced no reaction in the species concerned. Weir concluded that, although ants are incapable of perceiving sounds of audible pitch aerially transmitted, this is not true of those of higher frequency.

Weld (1899) carried on a more elaborate series of experiments on the sound-sensitivity of several ants, using instruments of several types to produce audible vibrations. More than eighty tests were conducted on the ants *Formica nitidiventris*, *Cremastogaster lineolata*, and *Aphaenogaster* sp. He obtained surprisingly uniformly positive reactions with these insects to the sound produced by a steel sounding bar of a frequency of 4096, a small bottle, tin and wooden whistles, and a tuning fork sounding middle A. The ants were usually in contact with glass, it is to be noticed, either in tubes suspended in the air, or in nests covered with glass plates. Weld concluded that the power of perception of vibrations of frequencies within the audible range was well developed, but did not state positively whether he thought these vibrations to be transmitted through air or solid media. He believed the phenomenon to be one of the perception of aerial waves, however, first, because he thought that he had detected a directional sense in the perception, second, because ants responding markedly to the sounds frequently showed no response whatever to mechanical shocks intentionally produced. He also believed that the nests which he used were insulated sufficiently against vibrations directly transmitted through material media (usually by suspension in the air by a thread or cord). Weld's results were confirmed by Miss Wagner (Metcalf, 1900), who found that a single species of ant (not mentioned) housed in an artificial nest (Lubbock type?) over a water

moat responded markedly to notes of a single pitch (not given) sounded on a whistle or violin, even though those instruments were held as much as fifteen feet from the nest.

In striking contrast to the results obtained by Weld were those of Miss Fielde and Parker (1904). These workers carried out a very complete series of experiments with a piano, violin, and Galton whistle, collectively producing sounds ranging from frequencies of 27 to 60,000 per second. Eight species of ants, including three subfamilies were used: *Camponotus pennsylvanicus*, *Formica sanguinea*, *Formica fusca subsericea*, *Lasius umbratus*, *Lasius latipes*, *Stenamma fulvum*, *Cremastogaster lineolata*, and *Stigmatomma pallipes*. The nests containing these species were protected from drafts, and were rested on thick paper, open connection being maintained between the air of the nest and that of the room in which the work was carried on. No positive reaction whatever was recorded in the course of an exhaustive series of tests. Several questionable reactions were seen, but these were not repeated on repetition of the note which had evoked them. In contrast to these results, Fielde and Parker obtained uniformly positive reactions when the same series of tests was repeated with the nests arranged so that they were directly in contact with vibrating mechanical media. The authors concluded that the ants experimented upon were incapable of perceiving aerial vibrations within the very large range tested, but, as would be expected, were extremely sensitive to material vibrations of the same frequency.

Metcalf (1900), Wasmann (1893), and Turner (1907), working with various species of ants, all obtained positive reactions to sounds of variable pitch. The experiments of the last-named are especially interesting. *Formica fusca* and *Formica sanguinea* reacted decidedly and with considerable uniformity to sounds ranging from 256 to 4138 vibrations per second. The nests of these insects were mounted on cotton and felt and sufficient precaution taken, Turner believed, to exclude mechanical shock.

Wheeler has given the weight of his opinion to the belief that sonant vibrations are, at least to some extent, aerially perceived, since without such a supposition the remarkable coordination of many Myrmicine ants in the face of situations which cause them to stridulate violently would be very difficult to explain. Perception of a stridulatory sound through material media under such conditions would be a process hard to understand.

Methods

In the face of such remarkably diverse evidence and such a complete conflict of opinion among investigators of the subject, it has been the purpose of the following paper to reconsider the question from a very limited viewpoint, and to attempt to add some evidence of at least small value which might prove of some use to those in future concerned with the problem. The primary object of the work was made the determination of the power of certain ants to perceive sounds which, with as great a degree of certainty as could be experimentally obtained, were actually transmitted wholly through air. No attempt was made to establish the limits of this power of perception, if it existed, and all tests were carried out within a very limited range of frequency, bounded at the one extreme by a frequency of 261.6 vibrations per second, at the other by one of 523.3/second, and including only the usual chromatic scale, C to C, A 440 pitch. The instrument used throughout in sound-production was a carefully calibrated pitchpipe.

It is clear that vibrations resulting from the production of sound which may be perceived by ants as vibrations in material media may arise in two ways. The mechanical agitation set up at the sound-producer may be transmitted directly, through an unbroken chain of fairly rigid media, to the ants, where it will be quickly perceived in the fashion demonstrated by Miss Fielde and Parker. Any break in the chain of rigid media will result in a serious diminution of the effect at the further end of the chain. Such insulation is not difficult to introduce, and has been supplied in one form or another by most investigators.

On the other hand, it is not difficult, of course, to obtain mechanical vibrations in a rigid medium entirely insulated by air from a sound-producer, particularly with sounds of lower pitch. Such vibrations in artificial nests made of fairly incompressible solids are usually forced, rarely and only coincidentally actually completely resonant, but it is quite conceivable that they may reach proportions readily detected mechanically by ants, with their excessively delicate tactile sense. No amount of insulation can eliminate this factor, so long as the ants are in contact with incompressible or slightly compressible solids. Only when such media have been wholly eliminated, and abundant insulation supplied in addition, can any certainty be expressed that ants, reacting to a certain sound, have perceived it aerially. Such aerial perception, of course, would imply the forced vibration of some portion of the insect's own body, in all probability

the delicate chitinous integument overlaying the terminations of the chordontal organs—a process analagous to our own perception of sounds, so far as the factor of forced vibrations is concerned.

With this fact in view, three types of nests were constructed for use in the present tests. The first was designed to eliminate only the factor of mechanical shock transmitted by solids from the sound-producer to the ants. It consisted of a glass nest of the Lubbock type, earth-filled and 5.1 x 15.3 centimeters square. This case was mounted on sixty-four layers of Turkish toweling, mounted in turn on a baize-covered card-table. A microscope slide-cover, circular in form and 1.8 centimeters in diameter, was given a very thin coating of silver in a solution of ammoniacal silver nitrate reduced with formaldehyde, and mounted with a drop of sealing-wax on a fine wire 13.0 centimeters in length. The whole was then mounted, likewise with sealing-wax, on the glass cover of the nest, being fixed by the end further from the mirror near the edge of the cover, the line of the wire being vertical to the line of the edge, but in the plane of the cover. The plane of the mirror was perpendicular to the plane of the case, and it was projected, the wire being supported only at the end by which it was attached. Several mirror-wire attachments were used in the course of the tests. The first of these, whose mass was carefully measured, weighed 0.25775 ± 0.00005 grams. A beam from a tungsten-filament lamp was thrown on the oscillating mirror thus created, and the reflected ray brought to a focus upon a screen with a convergent lens. The screen was distant some 50 centimeters from the lens, and some 85 centimeters from the mirror.

It was hoped that this arrangement might provide a sensitive means of detecting mechanical shock of sufficient magnitude to pass through the toweling, if such shock were present, and in practice it proved to be very sensitive. Throughout, no mechanically transmitted vibration was detected, but slight vibrations of the mirror caused by the breath in sounding the pitchpipe were difficult to eliminate, although the pipe was sounded at a considerable distance.

Although sensitive in the detection of mechanical shock, the mirror and wire—a sort of crude optical telescope arrangement—were of too great mass to give any indication of the more minute forced vibrations which in all probability were consistently set up in the glass plates of the nest, and which, it seemed, might readily be perceived by the ants, especially as loose grains of earth of small mass might readily magnify them. The second type of container used, therefore, was designed to eliminate all mechanical vibrations, however produced. It consisted

of a block of soft putty, molded into chambers and galleries simulating those normally constructed by ants, and covered with a glass plate of the same dimensions, except where otherwise indicated, as those used in the preceding type of formicary. The putty nest was mounted in the same fashion as the glass type for testing, on sixty-four layers of toweling on a baize-covered table. No earth was included in the nest.

There remained the possibility that the putty in this type of chamber might be sufficiently firm to transmit a small amount of mechanical shock, or even to vibrate forcedly to a very slight extent. Again, the glass plate set over it might transmit mechanical vibrations of sufficient magnitude to be detected by the ants in the body of the nest. A third type of nest was constructed to eliminate this uncertainty, composed in the one case of four, in the other of six, layers of very soft cotton wadding, stitched together and sufficiently smooth on the inner surface to permit ready passage of the insects about the chamber, and to offer no difficulties for them in traversing its floor. The nest was covered with a sheet of glassine paper, laid loosely over its surface to protect the confined ants from drafts. When moistened on its inner surface, this container proved acceptable, and even agreeable, to most of the ants confined within it, though in a few cases it was necessary to replace individuals quite frequently, owing to the easy avenue of escape under the paper. This nest, like the others, was mounted on sixty-four layers of toweling on baize. The writer could see no possibility, in this arrangment, of the transmission of material vibrations to the ants, so long as they were not touching the covering paper. The nest was made sufficiently deep to eliminate this inconvenience. No earth was contained in it.

Finally, tests were made with several species inhabiting Lubbock earth-containing glass nests, six by eight inches square, which the individuals concerned had occupied for long periods of time, to check the influence of psychological factors affecting responses under new and unfamiliar conditions in the other cases. These nests were mounted in the same fashion as the preceding ones.

Twenty-five species of ants were used in the work: *Stigmatomma pallipes*, *Ponera coarctata pennsylvanica*, *Euponera gilva harnedi*, *Paraponera clavata*, *Odontomachus clarus*, *Odontomachus hastatus*, *Odontomachus chelifer*, *Ectatomma tuberculatum*, *Leptothorax acervorum canadensis* var. *yankeer*, *Leptothorax longispinosus*, *Myrmecina graminicola americana* var. *brevispinosa*, *Aphaenogaster fulva aquia*, *Myrmica scabrinodis sabuleti*, *Solenopsis molesta*, *Cremastogaster lineolata*,

Tapinoma sessile, *Prenolepis imparis*, *Camponotus castaneus americanus*, *C. herculeanus pennsylvanicus*, *C. herculeanus pennsylvanicus* var. *noveboracensis*, *Acanthomyops claviger*, *Lasius flavus nearcticus*, *Lasius niger americanus*, *Formica fusca subsericea*, and *Formica sanguinea rubicunda*. The Ponerine, Myrmicine, Dolichoderine and Formicine subfamilies were thus represented, and there were included entirely hypogaeic as well as epigaeic and semi-arboreal types from a rather wide range of habitat. The geographic range was similarly rather wide, extending from typically dominant circumpolar forms on the one hand, denizens of the open wood and field land of our northern or northwestern states, to species confined entirely to the jungles of the New World tropics on the other. Forms with both monomorphic and polymorphic workers were included, and the list contains a single species of honey ant. Through the use of such a range of habitat-groups and of conditions of social evolution it was hoped to justify some generalizations from the results.

The interpretation of response to sounds in ants is a very difficult thing to accomplish accurately, and, because no two species react in precisely the same fashion, it must remain an individual construction from observer to observer. This fact is probably one potent cause of the astonishing difference of observation recorded in the literature, even with ants of the same species responding to notes of the same pitch, as with the work of Miss Fielde and Parker (1904) on the one hand and that of Weld (1899) on the other on *Cremastogaster lineolata*. In the present case a very considerable effort was made, first, to eliminate all preconceived ideas as to the ability or inability of the ants to perceive aerial vibrations, and second, to estimate all responses very conservatively. These responses, when present, took a variety of forms. In retrosalient species, such as those of the genus *Odontomachus*, sudden complete divarication of the mandibles proved an important indication, and partial divarication was of value throughout. Antennal movements, particularly in the genera *Ponera*, *Euponera*, *Prenolepis*, *Lasius*, and *Formica*, often gave decided indication of reaction. Movements of the tarsi in consistent response were common in the genus *Formica*. They were rare or absent in the cotton nests, however, and may therefore have been an indication of the perception of forced vibrations mechanically received. More violent reactions, such as a starting forward, or oblique lunge, were very usual in *Formica subsericea*, and a short, sudden run directly forward, followed by persistent non-reaction for several tests, was not unusual with *Stigmatomma* and *Leptothorax*.

Reactions

Reactions or the results of tests were divided into four classes. The first, designated in the tables following by the figure 0, was considered as "no reaction." In the majority of cases so labeled, the ants, so far as could be detected, were perfectly indifferent to the sounds produced, but many very slight or uncertain reactions were relegated to this category. The second class, considered as embracing "slight possible reactions," and designated by the figure 1, included readily visible reactions which, however, were not repeated immediately on repetition of the note which had evoked them. Occasionally they were repeated on a third or fourth sounding, but insufficiently clearly to convince the observer of a positive reaction. Quite positive reactions veiled by other movements were also consigned to this class. The third division, designated by the figure 2, included "slight positive reactions." These were slight but definite movements, repeated consistently two or three times successively on successive sounding of a note and not otherwise, so as to leave little reasonable doubt as to their nature as true responses. Some of these were very impressive in their consistency and clear-cut character. The final class, that of "positive reactions," indicated by the figure 3, included movements whose significance was no more certain than those of the preceding class, but which were more striking, such as the run or lunge mentioned above. These were usually consistently repeated, but in a few timid species (*Leptothorax*) persistent hiding followed a marked reaction, and no response whatever could be evoked for several minutes.

Each of the thirteen notes of the C to C chromatic scale was sounded twice for each species in each type of nest, with an interval usually of five minutes or more between each recorded sounding, during which the ants concerned were kept in a silent place. Ordinarily this was achieved by mounting the nest concerned upon the stand used and immediately sounding a note, then leaving the case undisturbed and in silence for five minutes, after which the note was again sounded and the case removed to another room, while that containing another species was at once mounted and the process repeated. The note sounded immediately after each case was mounted is indicated in the following tables by the letter *M* preceding the time of the record. Glass cases, because of the difficulty of repeatedly focusing the pencil of light from the optical telescope upon the screen, were ordinarily left in place throughout the series, only a single species being tested at one time. With a few exceptions, therefore, the designation *M*

does not appear in these tests. For each record the note concerned was sounded two to five times, to determine the consistency of the reaction. Occasionally ants escaped at the moment of testing, or were too restless to yield reliable results, which cases are indicated in the tables by blanks. The minute stature of the workers of *Solenopsis molesta* made necessary a modification of the usual method in testing that species in glass and putty cases. Minute nests of both types were made up with microscope slides, and mounted on the stage of a low-power microscope. The microscope itself was mounted on the toweling, which should have excluded vibrations directly transmitted, but it is to be noticed that no screening was offered in this case for forced vibrations arising in the microscope stage. The visibility of the reactions of all species in the cotton nests, because of the brilliant white background, was much improved, and was sufficient with *S. molesta* to permit the reliable observation of reactions with the naked eye.

Results were obtained as shown in the following tables:

TABLE I

Reaction to Sound in Certain Ants

PONERINAE

Stigmatomma pallipes

	Class I (Glass)		Class II (Putty)		Class III (Cotton)	
Time	Frequency	Reaction	Time	Reaction	Time	Reaction
M 8:20	261.6 (C)	0	4:25		M 3:02	1
8:25		0	M 4:20	0	3:07	
M 8:30	277.2 (C#)	0	4:05	0	M 3:12	2
8:35		1	M 4:00	0	3:17	1
M 8:40	293.7 (D)	0	3:30	0	M 3:22	1
8:45		0	M 3:25		3:27	3
M 8:50	311.1 (D#)	0	3:15	1	M 3:37	1
8:55		0	M 3:10	1	3:42	1
M 9:00	329.6 (E)	0	2:55	0	M 3:47	2
9:05		0	M 2:50	0	3:52	2
M 9:10	349.2 (F)	3	2:25	0	M 3:57	1
9:15		1	M 2:20	0	4:02	1
M 9:20	370.0 (F#)	3	2:05	0	M 4:07	2
9:25		0	M 2:00	0	4:12	1
M 9:45	392.0 (G)	0	1:40	0	M 4:17	2
9:50		0	M 1:35	0	4:22	0
M 9:55	485.3 (G#)	0	1:30		M 4:27	2
10:00		0	M 1:15	0	4:32	2
M10:05	440.0 (A)	1	1:00	0	M 4:37	2
10:10		0	M12:55	0	4:42	1
M10:15	466.2 (Bb)	1	12:40	0	M 4:47	2
10:20		0	M12:35	1	4:52	0
M10:25	493.9 (B)	0	12:18	0	M 4:57	0
10:35		1	M12:12	2	5:02	1
M10:40	523.3 (C)	0	12:07		M 5:07	0
10:45		0	M10:45	3	5:12	0

Ponera coarctata pennsylvanica

	Class I (Glass)		Class II (Putty)		Class III (Cotton)	
Time	Frequency	Reaction	Time	Reaction	Time	Reaction
5:15	261.6 (C)	0	4:15	0	12:47	1
M 5:10		0	M 4:10	0	M12:42	0
5:05	277.2 (C#)	1	3:55	0	12:37	0
M 5:00		1	M 3:50	0	M12:32	0
4:55	293.7 (D)	1	3:35	0	12:27	0
M 4:50		0	M 3:30	0	M12:22	2
4:45	311.1 (D#)	0	3:15	0	12:17	0
M 4:40		0	M 3:10	0	M12:12	0
4:35	329.6 (E)	0	2:55	0	12:07	1
M 4:30		0	M 2:50	0	M12:02	1
4:25	349.2 (F)	0	2:35	1	11:57	0
M 4:20		0	M 2:30	0	M11:52	0
4:15	370.0 (F#)	0	2:15	0	11:47	0
M 4:10		1	M 2:10	3	M11:42	1
4:05	392.0 (G)	0	1:55	0	11:37	3
M 4:00		2	M 1:45	0	M11:32	0
3:55	415.3 (G#)	1	1:30	0	11:27	1
M 3:50		1	M 1:25	0	M11:22	0
3:45	440 (A)	0	1:10		11:17	1
M 3:40		1	M 1:05	0	M11:12	0
3:25	466.2 (Bb)	1	12:50	0	11:07	0
M 3:20		0	M12:45	0	M11:02	0
3:15	493.9 (B)	0	12:30	0	10:57	0
M 3:10		0	M12:25	0	M10:52	1
3:05	523.3 (C)	0	12:10	0	10:47	
3:00		0	M12:05	0	M10:42	3

	Class I (Glass)		Class II (Putty)		Class III (Cotton)	
Time	Frequency	Reaction	Time	Reaction	Time	Reaction
Euponera gilva harnedi						
12:45	261.6 (C)	0	4:10	0	M12:47	0
12:40		0	M 4:05	0	12:52	3
12:35	277.2 (C#)	0	3:50	0	M12:57	0
12:30		1	M 3:45	0	1:02	0
12:25	293.7 (D)	0	3:20	0	M 1:07	1
12:20		0	M 3:15	0	1:12	2
12:15	311.1 (D#)	0	3:00	1	M 1:17	1
12:10		0	M 2:55	0	1:22	0
12:05	329.6 (E)	0	2:40	0	M 1:27	0
12:00		0	M 2:25	0	1:32	0
11:55	349.2 (F)	0	2:10	1	M 1:37	0
11:50		0	M 2:05	0	1:42	0
11:45	370.0 (F#)	0	1:45	0	M 1:47	0
11:40		0	M 1:40	0	1:52	0
11:35	392.0 (G)	0	1:25	0	M 1:57	0
11:30		0	M 1:20	0	2:02	0
11:25	415.3 (G#)	0	1:05	1	M 2:07	0
11:20		0	M 1:00	1	2:12	0
11:15	440.0 (A)	0	12:45	1	M 2:17	1
11:10		0	M12:40	0	2:22	1
11:05	466.2 (Bb)	0	12:21	0	M 2:27	1
11:00		0	M12:19	0	2:32	0
10:45	493.9 (B)	1	11:10		M 2:37	0
10:40		3	M11:00	0	2:42	1
10:55		0	10:24	3	M 2:47	0
10:50		2	M10:15	2	2:52	0
Odontomachus clarus						
8:07	261.6 (C)	0	M 9:15	0	M 7:05	0[1]
8:12		0	9:20	0	7:10	0
8:17	277.2 (C#)	0	M 9:05	0	M 7:30	
8:22		0	9:10	1	7:35	0
8:27	293.7 (D)	0	M 9:25	0	M 8:10	
8:32		0	9:30	2	8:15	
8:37	311.1 (D#)	1	M 9:35	0	M 8:30	0
8:42		0	9:40	0	8:35	0
8:47	329.6 (E)	1	M 9:45	1	M 8:40	1
8:52		0	9:50	2	8:45	1
8:57	349.2 (F)	0	M 9:55	2	M 8:50	2
9:02		0	10:00	0	8:55	0
9:07	370.0 (F#)	0	M10:05	0	M 9:20	0
9:17		0	10:10	0	9:25	1
9:32	392.0 (G)	0	M10:15	0	M 9:30	0
9:37		0	10:20	0	9:35	0
9:42	415.3 (G#)	0	M10:25	0	M 9:40	0
9:47		1	10:30	0	9:45	0
9:52	440.0 (A)	0	M10:35	0	M 9:50	0
11:22		0	10:40	2	9:55	0
11:27	466.2 (Bb)	0	M10:50	1	M10:00	0
11:32		0	10:55	0	10:05	0
11:37	493.9 (B)	1	M11:00	2	M10:10	0
11:42		0	11:05	2	10:15	
11:47	523.3 (C)	0	M11:10	2	M10:20	1
11:52		1	11:15	2	10:25	0

	Class I (Glass)		Class II (Putty)		Class III (Cotton)	
Time	Frequency	Reaction	Time	Reaction	Time	Reaction
Odontomachus hastatus						
8:20	261.6 (C)	0	4:20	0	M 8:12	1
8:15		0	M 4:15	0	8:17	0
8:10	277.2 (C#)	0	4:00	0	M 8:27	0
8:05		0	M 3:55	0	8:32	1
8:00	293.7 (D)	1	3:30	0	M 8:37	1
7:55		0	M 3:25	0	8:42	0
7:50	311.1 (D#)	0	3:10	0	M 8:47	0
7:45		0	M 3:05	0	8:52	0
7:40	329.6 (E)	1	2:50	0	M 8:57	0
7:35		1	M 2:45	0	9:02	0
7:30	349.2 (F)	0	2:20	1	M 9:07	0
7:25		0	M 2:15	0	9:12	0
7:20	370.0 (F#)	0	2:00	0	M 9:17	0
7:15		0	M 1:55	0	9:22	0
7:10	392.0 (G)	0	1:35	1	M 9:42	0
7:05		1	M 1:30	0	9:47	0
5:00	415.3 (G#)	0	1:15	0	M 9.52	0
4:55		0	M 1:10	0	9:57	0
4:50	440.0 (A)	0	12:55	1	M10:02	0
4:45		0	M12:50	0	10:07	1
4:40	466.2 (Bb)	0	12:35	0	M10:12	0
4:35		1	M12:29	0	10:17	0
4:30	493.9 (B)	0	M12:01–12:10	1	M10:22	1
4:25		0	M11:01	0	10:27	0
4:20	523.3 (C)	0	10:38	0	M10:32	1
4:15		0	M10:33	0	10:37	0
Odontomachus chelifer						
2:45	261.6 (C)	0	4:15	0	M 2:00	0
2:40		0	4:10	0	2:05	2
2:35	277.2 (C#)	0	3:55	0	M 2:10	1
2:30		0	3:50	1	2:15	1
2:25	293.7 (D)	0	3:25	0	M 2:20	0
2:20		0	M 3:20	0	2:25	0
2:15	311.1 (D#)	0	3:05	1	M 2:30	0
2:10		0	M 3:00	0	2:35	0
2:05	329.6 (E)	0	2:45	0	M 2:40	1
2:00		0	M 2:40	0	2:45	3
1:55	349.2 (F)	0	2:15	0	2:50	0
1:50		0	M 2:10	0	2:55	3
1:45	370.0 (F#)	1	1:50	0	3:00	1
1:40		0	M 1:45	0	3:05	3
1:35	392.0 (G)	0	1:30	0	3:10	3
1:30		0	M 1:25	0	3:15	1
1:25	415.3 (G#)	0	1:10	0	3:20	0
1:20		0	M 1:05	0	3:25	2
1:15	440.0 (A)	0	12:50	0	3:30	0
1:10		0	M12:45	0	3:35	1
1:05	466.2 (Bb)	0	12:28	0	3:40	3
1:00		0	M12:23	0	3:45	2
12:55	493.9 (B)	1	11:47	0	3:50	0
12:50		0	M11:38	0	3:55	1
12:45	523.3 (C)	1	M10:50	0	4:00	0
12:40		0	M10:30	1	4:05	0

[1] Mounted in this series in a two-dram vial, earth-containing, without wire attachment.

Paraponera clavata

Time	Class I (Glass) Frequency	Reaction	Class II (Putty) Time	Reaction	Class III (Cotton) Time	Reaction
9:07	261.6 (C)	1	M 9:20	0	12:55	0
9:12		1	9:25	0	M12:50	0
9:17	277.2 (C#)	0	M 9:10	0	12:45	0
9:22		0	9:15	0	M12:40	0
9:27	293.7 (D)	0	M 9:30	0	12:35	0
9:32		0	9:35	0	M12:30	0
9:37	311.1 (D#)	0	M 9:40	0	12:25	0
9:42		0	9:45	1	M12:20	0
9:47	329.6 (E)	0	M 9:50	0	12:15	0
9:52		0	9:55	0	M12:10	0
9:57	349.2 (F)	0	M10:00	0	12:05	0
10:02		0	10:05	1	M12:00	0
10:07	370.0 (F#)	0	M10:10	0	11:55	0
10:12		0	10:15	0	M11:50	0
10:17	392.0 (G)	0	M10:20	0	11:45	0
10:22		1	10:25	0	M11:40	0
10:27	415.3 (G#)	0	M10:30	0	11:35	0
10:32		0	10:35	0	M11:30	0
10:37	440.0 (A)	0	M10:45	0	11:25	0
10:42		0	10:50	1	M11:20	0
10:47	466.2 (Bb)	0	M10:55	1	11:17	0
10:52		0	11:00	0	M11:12	0
10:57	493.9 (B)	0	M11:05	0	11:07	0
11:02		0	11:10	0	M11:02	1
11:07	523.3 (C)	0	M11:15	0	10:57	0
11:12		1	11:20	0	M10:52	0

Ectatomma tuberculatum

Time	Class I (Glass) Frequency	Reaction	Class II (Putty) Time	Reaction	Class III (Cotton) Time	Reaction
10:22	261.6 (C)	0	M 8:50	0	M 8:52	1
10:17		2	8:55	0	8:57	2
10:12	277.2 (C#)	1	M 9:00	0	M 9:02	2
10:07		0	9:05	0	9:07	2
10:02	293.7 (D)	0	M 9:10	0	M 9:12	2
9:57		1	9:15	0	9:17	1
9:52	311.1 (D#)	1	M 9:20	0	M 9:22	2
9:47		1	9:25	0	9:27	1
9:42	329.6 (E)	0	M 9:30	1	M 9:32	1
9:37		0	9:35	0	9:37	2
9:32	349.2 (F)	1	M 9:40	0	M 9:42	2
9:27		1	9:45	0	9:47	1
9:22	370.0 (F#)	0	M 9:50	0	M 9:52	2
9:12		0	9:55	0	9:57	1
9:17	392.0 (G)	0	M10:00	0	M10:02	2
9:07		2	10:05	0	10:07	2
9:02	415.3 (G#)	1	M10:10	0	M10:12	2
8:57		0	10:15	0	10:17	0
8:52	440.0 (A)	0	M10:20	0	M10:22	2
8:47		0	10:25	0	10:27	2
8:42	466.2 (Bb)	0	M10:30	0	M10:32	0
8:37		0	10:35	0	10:37	2
8:32	493.9 (B)	0	M10:40	0	M10:42	1
8:27		2	10:45	0	10:47	2
8:22	523.3 (C)	1	M10:50	0	M10:52	2
8:13		0	10:50	0	10:57	0

MYRMICINAE

Myrmecina gramnicola americana var. brevispinosa

Time	Class I (Glass) Frequency	Reaction	Class II (Putty) Time	Reaction	Class III (Cotton) Time	Reaction
12:50	261.6 (C)	1	4:05	0	8:27	1
12:55		0	M 4:00	0	M 8:22	1
1:00	277.2 (C#)	0	3:45	0	8:17	1
1:05		0	M 3:40	0	M 8:12	2
1:10	293.7 (D)	0	3:25	0	8:07	0
1:15		0	M 3:20	0	M 8:02	0
1:20	311.1 (D#)	1	3:05	0	7:57	3
1:25		1	M 3:00	0	M 7:52	0
1:30	329.6 (E)	1	2:45	0	7:47	1
1:35		0	M 2:40	0	M 7:42	1
1:40	349.2 (F)	0	2:25	0	7:37	2
1:45		0	M 2:20	0	M 7:32	0
1:50	370.0 (F#)	0	2:05	0	7:27	1
1:55		0	M 2:00	0	M 7:22	0
2:00	392.0 (G)	2	1:40	0	7:17	1
2:05		1	M 1:35	0	M 7:12	0
2:10	415.3 (G#)	0	1:20	0	7:07	2
2:15		1	M 1:15	0	M 7:02	3
2:20	440.0 (A)	0	1:00	0	5:02	1
2:25		0	M12:55	0	M 4:57	0
2:40	466.2 (Bb)	0	12:40	0	4:47	0
2:45		0	M12:35	0	M 4:42	1
2:50	493.9 (B)	2	12:20	0	4:37	1
2:55		1	M12:15	0	M 4:32	2
3:00	523.3 (C)	0	12:00	0	4:27	3
3:05		0	M11:55	0	M 4:22	2

Leptothorax acervorum canadensis var. yankee

Time	Class I (Glass) Frequency	Reaction	Class II (Putty) Time	Reaction	Class III (Cotton) Time	Reaction
5:45	261.6 (C)	1	M 7:15	0	2:47	1
5:40		0	7:20	0	M 2:42	1
5:35	277.2 (C#)	1	M 7:40	0	2:37	0
5:30		0	7:45	0	M 2:32	0
5:25	293.7 (D)	0	M 8:00	0	2:27	0
5:20		0	8:05	0	M 2:22	0
5:15	311.1 (D#)	0	M 8:20	0	2:17	0
5:10		0	8:25	0	M 2:12	0
5:05	329.6 (E)	0	M 8:32	0	2:07	2
5:00		0	8:37	0	M 2:02	1
4:55	349.2 (F)	0	M 8:42	0	1:57	0
4:50		0	8:47	0	M 1:52	0
4:45	370.0 (F#)	0	M 8:52	0	1:47	1
4:40		0	8:57	0	M 1:42	2
4:35	392.0 (G)	0	M 9:22	0	1:37	2
4:30		0	9:27	0	M 1:32	2
4:25	415.3 (G#)	1	M 9:32	0	1:27	0
4:20		0	9:37	0	M 1:22	0
4:15	440.0 (A)	0	M 9:42	0	1:17	2
4:10		0	9:47	0	M 1:12	0
4:05	466.2 (Bb)	0	M 9:52	0	1:07	0
4:00		0	9:57	0	M 1:02	1
3:55	493.9 (B)	2	M10:02	0	12:57	3*
3:50		0	10:07	0	M12:52	0
3:45	523.3 (C)	0	M10:12	0	11:47	0
3:40		0	10:17	0	M11:42	2

* In this case the ant was resting on the inner surface of the glassine covering, rather than on the cotton itself.

	Class I (Glass)		Class II (Putty)		Class III (Cotton)	
Time	Frequency	Reaction	Time	Reaction	Time	Reaction
	Leptothorax longispinosus					
4:45	261.6 (C)	0	M 4:20	0	M 4:20	1
4:40		0	4:25	1	4:25	0
4:35	277.2 (C#)	0	M 4:30	0	M 4:30	1
4:30		0	4:35	1	4:35	0
4:25	293.7 (D)	0	M 4:40	0	M 4:40	1
4:20		0	4:45	0	4:45	0
4:15	311.1 (D#)	0	M 4:50	0	M 4:50	1
4:10		0	4:55	0	4:55	0
4:05	329.6 (E)	0	M 5:00	0	M 5:00	0
4:00		0	5:15	1	5:15	0
3:55	349.2 (F)	0	M 5:20	0	M 5:20	1
3:50		0	5:25	0	5:25	0
4:55	370.0 (F#)	0	M 5:30	0	M 5:30	1
3:45		0	5:35	0	5:35	1
4:50	392.0 (G)	0	M 5:40	0	M 5:40	1
3:40		0	5:45	1	5:45	2
3:35	415.3 (G#)	0	M 5:50	0	M 5:50	1
3:30		0	5:55	0	5:55	1
3:25	440.0 (A)	0	M 6:00	0	M 6:00	0
3:20		0	6:05	0	6:05	2
3:15	466.2 (Bb)	0	M 6:10	0	M 6:10	0
3:10		0	7:20	0	7:20	0
3:05	493.9 (B)	0	M 7:25	0	M 7:30	0
3:00		1	7:30	0	M 7:40	1
2:55	523.3 (C)	1	M 7:35	0	7:35	0
2:50		1	7:45	0	7:45	2
	Aphaenogaster fulva aquia					
2:32	261.6 (C)	0	3:35	0	3:42	1
2:37		0	M 3:30	0	M 3:37	2
2:42	277.2 (C#)	0	3:25	0	3:27	1
2:47		0	M 3:20	0	M 3:22	2
2:55	293.7 (D)	1	3:15	2	3:17	2
2:57		1	M 3:10	0	M 3:12	2
3:02	311.1 (D#)	0	3:05	0	3:07	2
3:07		2	M 3:00	0	M 3:02	0
3:12	329.6 (E)	0	2:55	0	2:57	1
3:17		0	M 2:50	0	M 2:52	2
3:22	349.2 (F)	1	2:45	1	2:47	2
3:27		0	M 2:40	0	M 2:42	2
3:32	370.0 (F#)	0	12:35	0	12:37	1
3:37		0	M12:30	0	M12:32	0
3:42	392.0 (G)	1	12:10	0	12:12	0
3:47		0	M12:05	0	M12:07	2
3:52	415.3 (G#)	0	12:00	1	12:02	1
3:57		1	M11:55	2	M11:57	3
4:02	440.0 (A)	0	11:50	0	11:52	
4:07		0	M11:45	0	M11:47	
4:15	466.2 (Bb)	1	11:40	0	11:42	0
4:17		0	M11:35	0	M11:37	2
4:22	493.9 (B)	0	11:30	1	11:32	3
4:37		2	M11:25	0	M11:27	2
4:42	523.3 (C)	1	11:20	2	11:22	2
4:47		0	M11:15	0	M11:17	1

	Class I (Glass)		Class II (Putty)		Class III (Cotton)	
Time	Frequency	Reaction	Time	Reaction	Time	Reaction
	Myrmica scabrinodis sabuleti					
12:50	261.6 (C)	3	2:12	0	M 8:12	1
12:55		1	M 2:07	2	8:17	2
1:00	277.2 (C#)	0	2:02	0	M 8:22	2
1:05		0	M 1:57	1	8:27	2
1:10	293.7 (D)	2	11:10		M 8:32	2
1:15		2	M11:05		8:37	2
1:20	311.1 (D#)	0	12:52	0	M 8:42	0
1:25		0	M12:47	1	8:47	2
1:30	329.6 (E)	0	12:42	0	M 8:52	2
1:35		2	M12:37	3	8:57	2
1:40	349.2 (F)	2	12:32	0	M 9:02	2
1:45		0	M12:27	1	9:07	2
1:50	370.0 (F#)	0	12:22	0	M 9:17	2
1:55		2	M12:17	1	9:22	2
2:00	392.0 (G)	0	12:12	0	M 9:37	2
2:05		1	M12:07	0	9:42	1
2:10	415.3 (G#)	0	12:02	0	M 9:47	0
2:15		0	M11:57	2	9:52	2
2:20	440.0 (A)	2	11:52	0	M11:22	1
2:25		1	M11:47	2	11:27	0
2:30	466.2 (Bb)	1	11:42	1	M11:32	0
2:35		2	M11:37	2	11:37	2
2:40	493.9 (B)	2	11:32	0	M11:42	2
2:45		2	M11:27	1	11:47	2
2:50	523.3 (C)	2	11:22	2	M11:52	2
2:55		2	M11:17	2	11:57	2
	Solenopsis molesta					
4:10	261.6 (C)	0	M 3:45	0	M 4:00	1
3:55		0	3:50	0	4:05	0
4:00	277.2 (C#)	0	M 3:55	0	M 4:10	0
3:55		0	4:00	0	4:15	0
3:45	293.7 (D)	0	M 4:05	0	M 4:20	0
3:40		0	4:10	0	4:25	0
3:35	311.1 (D#)	0	M 4:15	0	M 4:30	0
3:30		1	4:20	0	4:35	0
3:25	329.6 (E)	0	M 4:25	1	M 4:40	0
3:20		0	4:30	0	4:45	0
3:15	349.2 (F)	0	M 4:35	0	M 4:50	0
3:10		0	4:40	0	4:55	0
3:05	370.0 (F#)	0	M 4:45	1	M 5:00	0
3:00		1	4:50	0	5:05	0
2:55	392.0 (G)	0	M 4:55	0	M 5:10	0
2:50		0	5:00	0	5:15	0
2:45	415.3 (G#)	0	M 5:05	0	M 5:20	0
2:40		0	5:10	0	5:25	0
2:35	440.0 (A)	0	M 5:15	0	M 5:30	0
2:30		0	5:20	0	5:35	0
2:25	466.2 (Bb)	0	M 5:25	0	M 5:40	0
2:20		0	5:30	0	5:45	0
2:15	493.9 (B)	0	M 5:35	2	M 5:52	0
2:10		0	5:40	0	9:47	0
2:05	523.3 (C)	0	M 5:45	0	M 9:52	0
2:00		1	5:50	1	9:57	0

MYRMICINAE—Cont.

Cremastogaster lineolata

	Class I (Glass)		Class II (Putty)		Class III (Cotton)	
Time	Frequency	Reaction	Time	Reaction	Time	Reaction
2:30	261.6 (C)	0	3:35	0	3:37	0
2:35		0	M 3:30	0	M 3:32	0
2:40	277.2 (C#)	0	3:20	1	3:22	0
2:45		0	M 3:15	0	M 3:17	0
2:50	293.7 (D)	0	3:10	0	3:12	1
2:55		0	M 3:05	0	M 3:07	0
3:00	311.1 (D#)	1	3:00	0	3:02	0
3:05		1	M 2:55	0	M 2:57	0
3:10	329.6 (E)	0	2:50	0	2:52	0
3:15		0	M 2:45	0	M 2:47	2
3:20	349.2 (F)	1	2:40	0	2:42	1
3:25		0	M 2:35	1*	M 2:37	1
3:30	370.0 (F#)	0	12:15	0	12:17	0
3:35		1	M12:10	0	M12:12	0
3:40	392.0 (G)	0	12:05	0	12:07	0
3:45		1	M12:00	0	M12:02	0
3:50	415.3 (G#)	1	11:55	0	11:57	0
3:55		0	M11:50	0	M11:52	0
4:00	440.0 (A)	0	11:45	0	11:47	2
4:05		0	M11:40	1	M11:42	1
4:10	466.2 (Bb)	1	11:35	0	11:37	0
4:15		0	M11:30	0	M11:32	0
4:20	493.9 (B)	0	11:25	0	11:27	2
4:35		2	M11:20	0	M11:22	0
4:40	523.3 (C)	0	11:15	0	11:17	0
4:45		0	M11:10	1	M11:12	0

DOLICHODERINAE

Tapinoma sessile

10:35	261.6 (C)	0	M 3:40	1	M 3:42	0
10:30		0	3:45	1	3:47	0
10:25	277.2 (C#)	0	M 3:47	0	M 3:52	0
10:20		0	3:52	0	3:57	0
10:15	293.7 (D)	0	M 3:57	0	M 4:02	1
10:10		0	4:02	1	4:07	0
10:05	311.1 (D#)	0	M 4:07	0	M 4:12	0
10:00		2	4:12	0	4:17	0
9:55	329.6 (E)	1	M 4:17	0	M 4:22	1
9:50		0	4:22	0	4:27	2
9:45	349.2 (F)	0	M 4:27	0	M 4:32	0
9:40		0	4:32	0	4:37	0
9:35	370.0 (F#)	0	M 4:37	1	M 4:42	1
9:30		0	4:42		4:47	0
9:15	392.0 (G)	0	M 4:47	0	M 4:52	1
6:10		0	4:52	0	4:57	0
6:00	415.3 (G#)	0	M 4:57	0	M 5:02	1
5:55		0	5:02	0	5:07	1
5:50	440.0 (A)	0	M 5:07	0	M 5:12	1
5:45		0	5:12	0	5:17	0
5:40	466.2 (Bb)	0	M 5:17	0	M 5:22	1
5:35		0	5:22	0	5:27	1
5:30	493.9 (B)	0	M 5:27	0	M 5:32	1
5:25		0	5:32	0	5:37	0
5:20	523.3 (C)	0	M 5:37	0	M 5:42	0
5:15		0	5:42	0	5:47	0

* Response in this case violent stridulation.

FORMICINAE

Prenolepis imparis

	Class I (Glass)		Class II (Putty)		Class III (Cotton)	
Time	Frequency	Reaction	Time	Reaction	Time	Reaction
8:35	261.6 (C)	1	2:30	2	12:42	2
8:30		0	M 2:25	2	M12:37	2
8:25	277.2 (C#)	2	2:20	0	12:32	2
8:20		2	M 2:15	0	M12:27	2
8:15	293.7 (D)	0	2:10	1	12:22	2
8:10		2	M 2:05	0	M12:17	2
8:05	311.1 (D#)	1	2:00	2	12:12	0
8:00		2	M12:55	2	M12:07	0
7:55	329.6 (E)	1	12:50	2	12:02	2
7:50		0	M12:45	1	M11:57	2
7:40	349.2 (F)	0	12:40	2	11:52	2
6:10		0	M12:35	0	M11:47	2
6:05	370.0 (F#)	0	12:30	2	11:42	2
6:00		2	M12:25	2	M11:37	2
5:55	392.0 (G)	2	12:20	3	11:32	2
5:50		1	M12:15	1	M11:27	2
5:45	415.3 (G#)	1	12:10	2	11:22	2
5:40		2	M12:05	1	M11:17	2
5:35	440.0 (A)	2	12:00	2	11:12	2
5:30		2	M11:55	1	M11:07	2
5:25	466.2 (Bb)	3	11:50	2	11:02	2
5:20		2	M11:45	3	M10:57	2
5:15	493.9 (B)	1	11:40	2	10:52	2
5:10		2	M11:35	0	M10:47	1
5:05	523.3 (C)	3	11:30	2	10:42	3
5:00		1	M11:25	2	M10:37	2†

Camponotus castaneus americanus

10:25	261.6 (C)	1	M 7:25	0	5:07	0
10:20		1	7:30	0	M 5:02	1
10:15	277.2 (C#)	0	M 7:35		4:57	2
10:10		1	7:40		M 4:52	1
10:05	293.7 (D)	0	M 7:45	0	4:47	0
10:00		0	7:50	0	M 4:42	1
9:55	311.1 (D#)	3	M 8:25	0	4:37	1
9:50		1	8:30	0	M 4:32	1
9:45	329.6 (E)	0	M 8:37	2	4:27	0
9:40		0	8:42	0	M 4:22	0
9:35	349.2 (F)	0	M 8:47	0	4:17	1
9:30		0	8:52	0	M 4:12	0
9:25	370.0 (F#)	1	M 8:57	0	4:07	0
9:20		1	9:02	3	M 4:02	0
9:15	392.0 (G)	1	M 9:27	0	3:57	0
9:10		0	9:32	0	M 3:52	0
9:05	415.3 (G#)	0	M 9:37	0	3:47	0
9:00		0	9:42	0	M 3:42	0
8:55	440.0 (A)	0	M 9:47	0	3:37	1
8:50		1	9:52	0	M 3:27	1
8:45	466.2 (Bb)	1	M 9:57	0	3:22	1
8:40		1	10:02	0	M 3:17	2
8:35	493.9 (B)	0	M10:07	0	3:12	1
8:30		0	10:12	0	M 3:07	1
8:25	523.3 (C)	2	M10:17	0	3:02	
8:20		0	10:22		M 2:57	0

† Ant resting on glassine in this case.

Camponotus herculeanus pennsylvanicus

Time	Class I (Glass) Frequency	Reaction	Class II (Putty) Time	Reaction	Class III (Cotton) Time	Reaction
4:10	261.6 (C)	0	M 9:55	0	M 9:55	0
3:55		0	10:00	0	10:00	0
4:00	277.2 (C#)	0	M10:05	0	M10:10	1
3:50		0	10:07	0	10:15	0
3:45	293.7 (D)	0	M10:10	1	M10:20	2
3:40		0	10:15	1	10:25	1
3:35	311.1 (D#)	0	M10:20	0	M10:30	0
3:30		1	10:25	0	10:35	0
3:25	329.6 (E)	0	M10:30	0	M10:40	1
3:20		0	10:35	0	10:45	2
3:15	349.2 (F)	0	M10:40	0	M10:50	2
3:10		0	10:45	0	10:55	2
3:05	370.0 (F#)	0	M10:50	1	M11:00	2
3:00		0	10:55	1	11:05	1
2:55	392.0 (G)	1	M11:00	0	M11:10	2
2:50		0	11:05	0	11:15	1
2:45	415.3 (G#)	0	M11:10	0	M11:20	2
2:40		0	11:15	0	11:25	1
2:35	440.0 (A)	0	M11:20	0	M11:30	3
2:30		0	11:25	0	11:35	0
2:25	466.2 (Bb)	0	M11:30	0	M11:40	0
2:20		1	11:35	1	11:45	0
2:15	493.9 (B)	0	M11:40	0	M11:50	0
2:10		1	11:45	1	11:55	0
2:05	523.3 (C)	0	M11:50	0	M12:00	0
2:00		1	11:55	0	12:05	0

Camponotus herculeanus pennsylvanicus var. noveboracensis

Time	Class I (Glass) Frequency	Reaction	Class II (Putty) Time	Reaction	Class III (Cotton) Time	Reaction
10:27	261.6 (C)	1	2:07	0	M12:52	0
10:22		1	M 2:02	0	12:57	0
10:17	277.2 (C#)	0	1:57	0	M 1:02	0
10:12		0	M12:52	0	1:07	0
10:07	293.7 (D)	0	12:47	0	M 1:12	0
10:02		1	M12:42	0	1:17	0
9:57	311.1 (D#)	0	12:37	0	M 1:22	0
9:52		0	M12:32	1	1:27	0
9:47	329.6 (E)	0	12:27	0	M 1:32	0
9:42		2	M12:22	0	1:37	0
9:37	349.2 (F)	0	12:17	0	M 1:42	2
9:32		0	M12:12	0	1:47	0
9:27	370.0 (F#)	0	11:47	0	M 1:52	0
9:22		0	M11:42	0	1:57	0
9:17	392.0 (G)	0	11:37	0	M 2:02	0
9:12		1	M11:32	0	2:07	0
9:07	415.3 (G#)	0	11:27	0	M 2:12	0
9:02		1	M11:22	0	2:17	1
8:57	440.0 (A)	0	12:07	0	M 2:22	1
8:52		0	M12:02	0	2:27	2
8:47	466.2 (Bb)	0	11:15	0	M 2:42	0
8:42		0	M11:10	0	2:47	0
8:37	493.9 (B)	1	11:05	0	M 2:52	2
8:32		0	M11:00	0	2:57	0
8:27	523.3 (C)	0	10:55	2	M 3:02	0
8:22		1	M10:50	0	3:07	0

Acanthomyops claviger

Time	Class I (Glass) Frequency	Reaction	Class II (Putty) Time	Reaction	Class III (Cotton) Time	Reaction
10:20	261.6 (C)	0	8:22	0	5:22	0
10:15		0	M 8:17	0	M 5:17	0
10:10	277.2 (C#)	0	8:12	0	5:12	0
10:05		0	M 8:07	0	M 5:07	1
9:55	293.7 (D)	0	8:02	1	5:02	0
10:00			M 7:57	0	M 4:57	0
9:50	311.1 (D#)	0	7:52	1	4:52	1
9:45		0	M 7:47	0	M 4:47	0
9:40	329.6 (E)	0	7:42	0	4:42	0
9:35		0	M 7:37	0	M 4:37	0
9:30	349.2 (F)	0	7:32	0	4:32	1
9:25		0	M 7:27	0	M 4:27	0
9:20	370.0 (F#)	0	7:22	0	4:22	0
9:10		1	M 7:17	1	M 4:17	0
9:15	392.0 (G)	0	7:12	0	4:12	0
9:05		0	M 7:07	0	M 4:07	0
9:00	415.3 (G#)	0	7:02	0	4:02	0
8:55		0	M 5:02	0	M 3:57	0
8:50	440.0 (A)	0	4:57	0	3:52	0
8:45		0	M 4:52	0	M 3:47	0
8:40	466.2 (Bb)	0	4:42	0	3:42	0
8:35		0	M 4:37	0	M 3:37	0
8:30	493.3 (B)	0	4:32	0	3:32	0
8:25		0	M 4:27	0	M 3:27	1
8:20	523.3 (C)	0	4:22	2	3:12	0
8:15		0	M 4:17	0	M 3:07	1

Lasius flavus nearcticus

Time	Class I (Glass) Frequency	Reaction	Class II (Putty) Time	Reaction	Class III (Cotton) Time	Reaction
8:05	261.6 (C)	0	4:10	1*	5:27	0
8:10		0	M 4:05	0	M 5:22	1
8:15	277.2 (C#)	1	3:50	0	5:17	0
8:20		1	M 3:45	0	M 5:12	0
8:25	293.7 (D)	0	3:30	0	5:07	1
8:30		0	M 3:25	1*	M 5:02	0
8:35	311.1 (D#)	0	3:10	0	4:57	0
8:40		0	M 3:05	1*	M 4:52	0
8:45	329.6 (E)	0	2:50	0	4:37	0
8:50		0	M 2:45	0	M 4:32	0
8:55	349.2 (F)	0	2:30	0	4:27	1
9:00		1	M 2:25	1	M 4:22	0
9:05	370.0 (F#)	2	2:10	0	4:17	0
9:15		0	M 2:05	0	M 4:12	0
9:30	392.0 (G)	0	1:45	0	4:07	0
9:35		0	M 1:40	0	M 4:02	0
9:40	415.3 (G#)	0	1:25	0	3:57	0
9:45		1	M 1:20	0	M 3:52	0
9:50	440 (A)	2	1:05	1	3:47	1
11:20		2	M 1:00	1*	M 3:42	0
11:25	466.2 (Bb)	0	12:45	0	3:37	0
11:30		0	M12:40	0	M 3:32	0
11:35	493.3 (B)	1	12:25	1	3:27	0
11:40		0	M12:20	0	M 3:22	1
11:45	523.3 (C)	1	12:05	0	3:17	0
11:50		2	M12:00	0	M 3:12	0

* Ant in contact with a small grain of earth accidentally introduced.

Time	Class I (Glass) Frequency	Reaction	Class II (Putty) Time	Reaction	Class III (Cotton) Time	Reaction
	Lasius niger americanus					
8:45	261.6 (C)	3	4:00	0	M12:47	0
8:50		3	M 3:55		12:52	2
9:00	277.2 (C#)	2	3:40	0	M12:57	2
9:05		2	M 3:35	0	1:02	1
9:10	293.7 (D)	0	3:20	0	M 1:07	1
9:15		2	M 3:15	0	1:12	2
9:20	311.1 (D#)	2	3:00	0	M 1:17	2
9:25		2	M 2:55	0	1:22	1
9:30	329.6 (E)	1	2:40	0	M 1:27	0
9:35		0	M 2:35	0	1:32	2
9:40	349.2 (F)	0	2:20	1	M 1:37	0
9:45		0	M 2:15	0	1:42	1
9:50	370.0 (F#)	1	2:00	0	M 1:47	2
9:55		0	M 1:55	0	1:52	2
10:00	392.0 (G)	1	1:35	0	M 1:57	1
10:05		2	M 1:30	0	2:02	1
10:10	415.3 (G#)	1	1:15	0	M 2:07	2
10:15		1	M 1:10	0	2:12	0
10:20	440.0 (A)	1	12:55	0	M 2:17	2
10:25		2	M12:50	0	2:22	1
10:30	466.2 (Bb)	2	12:35	0	M 2:27	2
10:35		2	M12:30	0	2:32	1
10:40	493.3 (B)	0	12:15	1	M 2:47	2
10:45		2	M12:10	0	2:52	2
10:50	523.3 (C)	1	11:55	0	M 2:57	2
10:55		1	M11:50	1	3:02	2
	Formica fusca subsericea					
2:50	261.6 (C)	0	M 7:10	0	M12:52	2
2:55		1	7:15	0	12:57	0
3:00	277.2 (C#)	0	M 7:35	2	M 1:02	2
3:05		1	7:20	2	1:07	2
3:10	293.7 (D)	0	M 7:55	2	M 1:12	2
3:15		0	8:00	2	1:17	2
3:20	311.1 (D#)	0	M 8:15	0	M 1:22	0
3:25		0	8:20	2	1:27	1
3:30	329.6 (E)	0	M 8:35	1	M 1:32	0
3:35		0	8:40	0	1:37	2
3:40	349.2 (F)	0	M 8:45	0	M 1:42	0
3:45		0	8:50	2	1:47	3
3:50	370.0 (F#)	0	M 8:55	0	M 1:52	2
3:55		0	9:20	1	1:57	3
4:00	392.0 (G)	0	M 9:25	0	M 2:02	1
4:05		0	9:30	3	2:07	2
4:10	415.3 (G#)	0	M 9:35	3	M 2:12	1
4:15		0	9:40	0	2:17	3
4:20	440.0 (A)	1	M 9:45	2	M 2:22	3
4:25		0	9:50	3	2:27	2
4:30	466.2 (Bb)	0	M 9:55	0	M 2:32	2
4:35		0	10:00	0	2:37	1
4:40	493.9 (B)	0	M10:05	3	M 2:42	2
4:45		0	10:10	1	2:47	1
4:50	523.3 (C)	0	M10:15	2	M 2:52	0
4:55		1	10:20	0	2:57	0

Time	Class I (Glass) Frequency	Reaction	Class II (Putty) Time	Reaction	Class III (Cotton) Time	Reaction
	Formica sanguinea rubicunda					
4:05	261.6 (C)	2	M 8:55	1	M 8:57	0
4:00		1	9:00	0	9:02	0
3:55	277.2 (C#)	0	M 9:05	1	M 9:07	0
3:50		1	9:10	0	9:12	0
3:45	293.7 (D)	0	M 9:15	1	M 9:17	0
3:40		1	9:20	0	9:22	0
3:35	311.1 (D#)	2	M 9:25	1	M 9:27	1
3:30		0	9:30	1	9:32	1
3:25	329.6 (E)	0	M 9:35	1	M 9:37	0
3:20		0	9:40	2	9:42	0
3:15	349.2 (F)	2	M 9:45	0	M 9:47	1
3:10		2	9:50	2	9:52	0
3:05	370.0 (F#)	2	M 9:55	1	M 9:57	0
3:00		0	10:00	0	10:02	0
2:50	392.0 (G)	1	M10:05	2	M10:07	0
6:12		1	10:10	2	10:12	0
6:02	415.3 (G#)	1	M10:15	2	M10:17	0
5:57		0	10:20	0	10:22	1
5:52	440.0 (A)	1	M10:25	2	M10:27	2
5:47		2	10:30	2	10:32	0
5:42	466.2 (Bb)	2	M10:35	2	M10:37	2
5:37		2	10:40	2	10:42	0
5:32	493.9 (B)	0	M10:45	2	M10:47	1
5:27		0	10:50	2	10:52	1
5:22	523.3 (C)	1	M10:55	2	M10:57	0
5:17		1	11:00	2	11:02	0

TABLE II

Reactions in Glass Nests Previously Inhabited

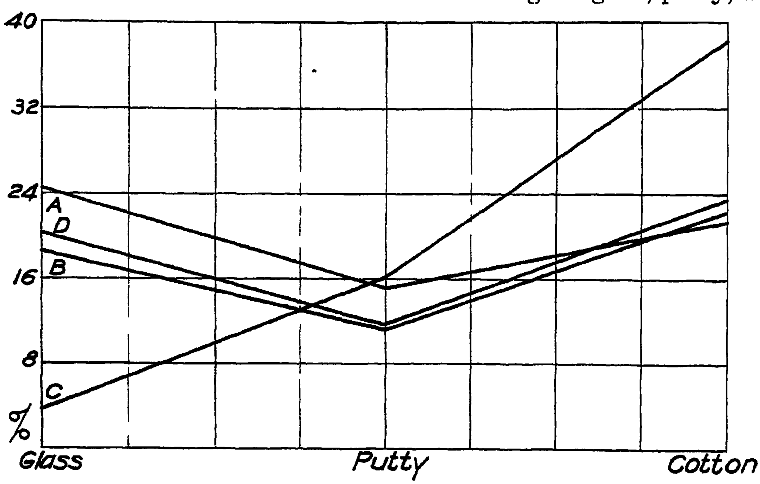
Stigmatomma pallipes*			Euponera gilva harnedi§		Odontomachus hastatus†	
8:47	261.6 (C)		2:52	1	8:42	1
M8:42		1	M 2:47	2	M 8:37	0
8:37	277.2 (C#)	0	2:42	0	8:32	0
M8:32		1	M 2:37	1	M 8:27	0
8:27	293.7 (D)	0	2:32		8:22	0
M8:22		1	M 2:27	2	M 8:17	0
8:17	311.1 (D#)	1	2:22	2	8:12	0
M8:12		0	M 2:17	1	M 8:07	0
8:07	329.6 (E)	1	2:12	2	8:02	0
M8:02		0	M 2:07	1	M 7:57	0
7:57	349.2 (F)	0	2:02	1	6:17	0
M7:52		2	M 1:57	0	M 6:12	0
6:12	370.0 (F#)	1	1:52	2	6:07	0
M6:07		0	M 1:47	1	M 6:02	0
6:02	392.0 (G)	2	1:42	2	5:57	0
M5:57		0	M 1:37	1	M 5:52	0
5:52	415.3 (G#)	2	1:32	2	5:47	0
M5:47		0	M 1:27	1	M 5:42	0
5:42	440.0 (A)	1	1:22	1	5:37	0
M5:37		1	M 1:17	1	M 5:32	0
5:32	466.2 (Bb)	2	1:12	0	5:27	0
M5:27		2	M 1:07	0	M 5:22	0
5:22	493.9 (B)	2	M12:57	1	5:17	0
M5:17		1	1:02		M 5:12	0
5:12	523.3 (C)	2	12:52	2	5:07	1
M5:07		2	M12:47	2	M 5:02	0

Ectatomma tuberculatum‡			Leptothorax acervorum canadensis var. vankeeri†		Camponotus castaneus americanus†	
7:20	261.6 (C)	3	M 2:52	2	12:57	2
7:25		2	2:57	2	1:02	0
7:30	277.2 (C#)	0	M 3:02	3	3:07	0
7:35		2	3:07	0	3:12	0
7:40	293.7 (D)	1	M 3:12	3	3:17	2
7:45		1	3:17	0	3:22	0
7:50	311.1 (D#)	0	M 3:22	0	3:27	0
7:52			3:27	0	3:32	0
7:55	329.6 (E)	2	M 3:32	0	3:37	1
8:00		2	3:37	0	3:42	0
8:05	349.2 (F)	1	M 3:42	1	3:47	0
8:15		1	3:47	2	3:52	0
8:25	370.0 (F#)	1	M 3:52	1	3:57	0
8:30		0	3:57	0	4:02	0
8:40	392.0 (G)	1	M 4:02	0	4:07	0
8:50		2	4:07	1	4:12	0
8:55	415.3 (G#)	0	M 4:12	2	4:17	0
9:00		0	4:17	0	4:22	0
9:05	440.0 (A)	2	M 4:22	0	4:27	0
9:10		1	4:27	1	4:32	0
9:20	466.2 (Bb)	1	M 4:32	2	4:37	1
9:25		2	4:37	2	4:42	0
9:30	493.2 (B)	2	M 4:42	1	4:47	0
9:35		0	4:47	2	4:52	0
9:40	523.3 (C)	1	M 4:52	1	4:57	2
9:45		2	4:57	1	5:02	0

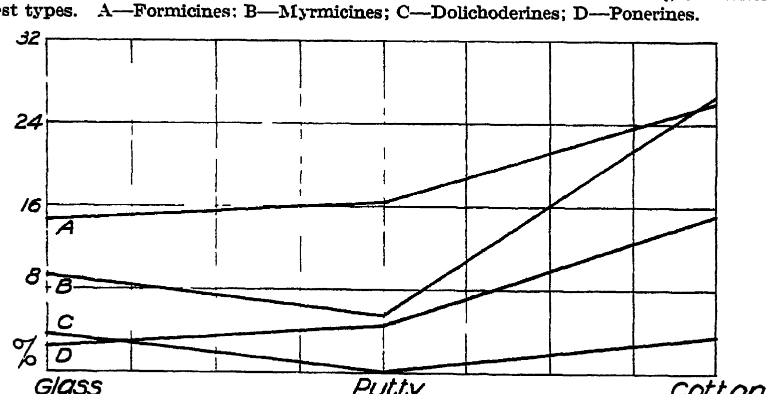
* Occupied six days before testing.
‡ Occupied about ten days before testing.
† Occupied nine days before testing.
§ Occupied four months before testing.

The total number of tests made and considered worthy of record in all nests was 2079. Of these, 44, or 2.12%, were markedly positive and accompanied by a striking reaction, 292, or 14.05%, were equally positive, but accompanied by slight though characteristic reactions, 402, or 19.34%, showed reactions which might be interpreted positively but which cannot be certainly so presented, and the remaining 1341, or 64.50%, were negative or only negligibly positive.

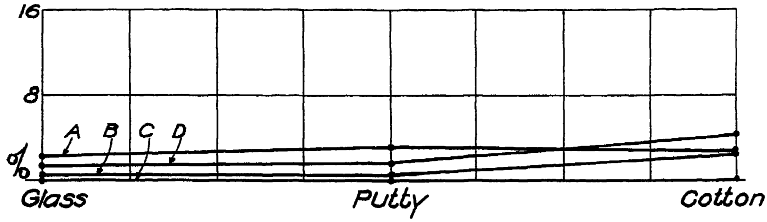
Slight possible (1), slight positive (2), and markedly positive (3) reactions were distributed, in percentage on the basis of the total number of tests conducted in each section among the glass, putty, and



GRAPH A. Percentages of slight possible reactions as distributed among the differing nest types. A—Formicines; B—Myrmicines; C—Dolichoderines; D—Ponerines.



GRAPH B. Percentages of slight positive reactions as distributed among the different nest types. A—Formicines; B—Myrmicines; C—Dolichoderines; D—Ponerines.



GRAPH C. Percentages of marked positive reactions as distributed among the different nest types. A—Formicines; B—Myrmicines; C—Dolichoderines; D—Ponerines.

cotton nests as shown in the accompanying graphs, the permanently established glass nests being excluded.

It will be noticed that there is no systematic deviation in the relative magnitude of the percentage of reactions for different types of nests within the same species throughout the series. The absence of such marked systematic deviation, which, it is believed by the writer, constitutes considerable evidence of the elimination of vitiating factors such as mechanical shock and drafts, throughout the tests, may perhaps be indicated more clearly in the tabulation below. Here the relative magnitude of the reaction percentages is given for each species in each type of nest, and for each type of possible or positive reaction. In the cases in which no reaction of the type considered took place in any of the three nests, the designated order for each type has been 3.

Reaction Type:	1 (Slight possible)			2 (Slight positive)			3 (Marked positive)		
Type of Nest·	Glass	Putty	Cotton	Glass	Putty	Cotton	Glass	Putty	Cotton
S. pallipes	2	3	1	3	2	1	1	3	2
P. coarctata	1	3	2	2	3	1	3	2	1
E. gilva	1	3	2	2	1	2	2	1	2
O. clarus	1	3	2	3	1	2	3	3	3
O. chelifer	2	2	1	2	2	1	2	2	1
O hastatus	2	3	1	3	3	3	3	3	3
P. clavata	1	1	2	3	3	3	3	3	3
E. tuberculatum	1	3	2	2	3	1	3	3	3
M. graminicola	2	3	1	2	3	1	2	2	1
L acervorum	2	3	1	2	3	1	2	2	1
L. longispinosus	3	2	1	2	2	1	3	3	3
A. fulva	1	3	2	3	2	1	2	2	1
M. scabrinodis	2	1	3	3	2	1	2	1	3
S. molesta	1	1	2	3	3	3	3	3	3
C. lineolata	1	2	2	2	3	1	3	3	3
T. sessile	3	2	1	1	2	1	3	3	3
P. imparis	1	2	3	3	2	1	1	1	2
C. americanus	2	3	1	3	2	1	2	1	3
C. pennsylvanicus	2	1	1	2	2	1	2	2	1
C. noveboracensis	1	3	2	2	2	1	3	3	3
A. claviger	3	2	1	2	1	2	3	3	3
L. nearcticus	2	1	3	1	2	2	3	3	3
L americanus	1	2	1	2	3	1	1	2	2
F. subsericea	2	3	1	3	2	1	2	1	1
F. sanguinea	1	2	3	2	1	3	3	3	3

The complete absence of a regular arrangement of the integers, which arrangement would be indicative of a systematic deviation, is evident.

Eliminating from consideration the glass and putty nests in which the factor of forced mechanical vibrations may not have been entirely excluded, an average of 22.98% of the tests made in cotton on the twenty-five species subjected to examination were recorded as slight possible, 21.20% as slight positive, and 3.28% as marked positive. Thirteen of the species, including the three subfamilies, were tested on four layers of cotton, while the remaining twelve were mounted over six layers. The general average of the three classes of reactions for the six-layer nests, in percentages relative to the total number of tests conducted, was 19.92% for slight possible, 30.57% for slight positive, and 3.19% for marked positive. The general average for the six-layer nests for all three reaction-types was 54.68%, higher than the general average of the same reaction-types for both four-layer and six-layer nests, which was 47.46%. In other words, a larger number of positive reactions was recorded for the better insulated case, giving some indication that mechanically transmitted and forced vibrations had been eliminated to such an extent that additional insulation was not effective. It will be noticed that, with six layers of cotton insulation, the tested ants were considered to respond to the notes as sounded in more than half the total number of trials. The three species tested in which the reactions in all types of nests were the most striking—*Myrmica scabrinodis*, *Prenolepis imparis*, and *Formica subsericea*—were all included in the six-layer cotton tests.

No species failed entirely to give a slight possible reaction in a cotton nest. Only five species, two Ponerine, one Myrmicine, and two Formicine, failed to give slight positive reaction, while four Ponerines, four Myrmicines, one Dolichoderine and six Formicines failed to react markedly. The general distribution of the positive reactions through the subfamilies is of interest.

A summary of the data shown and of the reasons presented lead to the belief and conclusion on the part of the writers that a definite power to perceive aerial vibrations within the C to C chromatic scale, A 440 pitch, exists in the twenty-five species of ants tested. It is the personal belief of the authors that the power will be found quite general in the *Formicidae*, and of wider scope than the sound-range used here could test.

Significance of Aerial Vibrations under Normal Conditions

Although the foregoing tests render highly probable the existence of a power to perceive certain sonant aerial vibrations among certain of the Formicidae, they by no means, it is believed, indicate that such a power is habitually socially employed. The contrary seems to be indicated. No series of tests with similar species of ants, employing vibrations of the same frequency in material media, would show so high a percentage of negative results. Under such conditions, as Miss Fielde and others have shown, the percentage of non-reaction tends to diminish very close to zero. It therefore seems quite clear that the significance of aerial vibrations as messengers of danger in the normal life of an ant colony is very much less than that of vibrations in material media. It would seem very natural that ants under normal conditions, living in close contact with rigid or semi-rigid media and for the greater part of the time entirely enclosed within galleries and chambers of earth, carton, or silk—where, indeed, the need of perception of mechanical vibrations is greatest—should depend much more upon these media to transmit vibrations directly than upon the air-column of the long and tenuous galleries, habitually closed to the open air in any case with many species. It may well be inquired whether vibrations indicative of other than danger may not be habitually perceived in the same way. The stridulatory power, if of any social use as can hardly be denied, would certainly be exercised to greatest advantage within the crowded formicary, where the close proximity of material media capable of vibrating forcedly would be expected to influence the method of perception. The power of perception of purely aerial vibrations might then well be reserved for use outside the nest, or might lapse entirely under normal circumstances, being retained only as an archaic relict.

Such an assumption would lead the investigator to expect some divergence between the results obtained in the preceding tests for glass and putty nests. Although the possibility of the presence of forced vibrations existed in both types, it was much greater in the former and a greater number of positive reactions might be expected, therefore, in the glass than in the putty. The tests fulfilled this expectation. Thus an average of 29.34% of the tests made on ants enclosed in glass nests with the mirror attachment—cases to which they had been newly introduced and in which they might therefore be suspected to be reacting subnormally—evoked possible or positive response, while this was true of only 22.89% of the tests conducted

in putty. It is probable that the divergence would be greater than this if corrected, since the visibility was much poorer in the glass nests than in the putty and in very many cases the presence of abundant earth in the former so excited the instinct to excavate that ants which normally responded freely to sound-stimuli became so occupied in the feverish excavation of galleries as to ignore such stimuli altogether. It is impossible to evaluate this factor accurately, because of its infinite variability. An attempt to do so was made, as already shown, in the conducting of similar tests with similarly constructed earth-filled glass nests with which the individuals concerned were thoroughly familiar, and in which the nest-form had become fixed. The percentage of possible and positive reactions for six species in such nests was 52.62%, as against 25.65% for nests with which individuals of the same six species were unacquainted. The factor of novelty to surroundings, therefore, would seem to be a very considerable one indeed.

Sound-production

The existence of organs of sound-production in the *Locustidae, Gryllidae, Cicadidae*, and elsewhere has been held strong presumptive evidence of the habitual use of a power to perceive aerial vibrations in those insects. That this is not necessarily true of ants is suggested by the inferior development of the chordontal organs over those of other stridulating types. The fact that there is apparently neither increase nor diminution in the power to sense sonant aerial vibrations in the non-stridulating subfamilies is also suggestive. Thus 127 of the 309 reactions obtained for all species in the cotton nests, or 40.78%, were evoked from Formicine and Dolichoderine ants, subfamilies apparently non-stridulating throughout. Formicine and Dolichoderine ants composed, in the present instance, 40% of the species tested. *Stigmatomma pallipes*, although a Ponerine, lacks the stridulating file, as will later be shown, but reacted in 80% of the tests conducted on it. *Ponera coarctata* of the same subfamily, on the other hand, possesses a very beautifully developed stridulatory organ, yet reacted in but 40% of the tests. It is very difficult to establish any correlation between the power of sound-production and sensitiveness to aerial vibrations.

On the other hand, it is very clear that vibrations set up within the nest by stridulation are clearly perceived by other members of the colony, and that they may be of great psychological significance. Wheeler (1903) has shown the important social use to which such a power may be put, and its importance is very clearly indicated by the

beautiful parallel which exists between the development of the stridulatory organ and the state of social development in the *Ponerinae*. Sharp (1893), in his extremely comprehensive paper, finds the file, characteristically situated on the mid-dorsal surface of the third abdominal—in Myrmicines the first, in Ponerines the second gastric—segment where it is normally covered by the preceding segment, to be absent in several extremely primitive Ponerine ants. It is found to be wanting in several species of the genus *Myrmecia*, probably comprising the most generalized of all ants. It is also absent, according to Sharp, in an unidentified Cerapachyine ant, in which the structure of the pedicel is extremely generalized. In the somewhat more highly specialized genus *Dinoponera*, Sharp finds the file, as also in *Paltothyreus*, while in the genus *Ponera*, represented in Sharp's series by *P. contracta* and an unidentified species, it is extremely well developed.

The present writer has examined the file in a number of *Ponerinae*, both tropical and native to the northern United States, with confirmatory results. *Stigmatomma pallipes*, which, like all Amblyopone ants, possesses an even more primitive peduncular structure than the old genus *Cerapachys* of Sharp, shows no specialization of the normal, elongate finger-print pattern of the protected dorsal surface of the third abdominal segment. The same condition obtains with *Proceratium croceum* and *Pachycondyla harpax*, both primitive types. On the other hand, the file is well developed in *Ponera coarctata*, unquestionably on a higher social plane, in *Ectatomma tuberculatum*, in *Lobopelta elongata*, and in *Neoponera villosa*, in which active and highly specialized ant it presents a very beautiful appearance. It is well developed and of such magnitude as to be readily observable with the naked eye in *Paraponera clavata*.

The file is further specialized in the *Myrmicinae*, and comes to form a polished table sharply differentiated from the surrounding integument, as Janet (1894a) has shown for *Myrmica rubra* and Sharp for *Myrmica scabrinodis*, *Aphaenogaster barbara*, *Atta cephalates*, and *Atta* sp. and in the Pseudomyrmine ants *Pseudomyrma* sp., *Sima rufonigra*, and *Sima* sp. The writer has examined the file in *Atta texana*, *Pogonomyrmex moleficans*, *Myrmica scabrinodis sabuleti*, *Aphaenogaster fulva aquia*, *Leptothorax longispinosus*, and *Solenopsis molesta*, with perfectly confirmatory results. The ridges are perfectly regular in the more highly developed tribes, and so closely set together that a magnification of at least 140 diameters is necessary to distinguish them at all satisfactorily, while one of 37.5 diameters is often quite sufficient to produce a clear image of the details of the sculpture of the surrounding integument.

Together with the perfection of structure with social advancement has come perfection of usage. Many of the larger Ponerines stridulate very audibly, so that the character of the process is easy to study. *Paraponera clavata*, *Odontomachus clarus*, *Neoponera villosa*, and *Lobopelta elongata* were all found to utter but one or two, or at most three notes in a series, and were only heard to stridulate under the influence of gross stimuli. In sharp contrast to this behavior is that of Myrmicine ants. In the place of a single note, the Myrmicines utter a rapid series of them, varying in frequency with the species, as will shortly be shown, and of considerable duration. In tests shortly to be presented it was found that *Myrmica scabrinodis* was capable of sustaining a composite call of this type for 1.336 minutes, in which time 780 strokes of the gaster were counted. A wide range of stimuli will evoke stridulation in most Myrmicine ants, and some of these stimuli are very delicate. The sudden discovery of food, return to the nest after a prolonged absence, insistent solicitation of food by a sister, are all sufficient. Workers of *Leptothorax acervorum* have been seen by the writer to stridulate in the artificial nest merely while licking their own larvae to obtain the exudates of the ectoderm. It is indeed difficult to believe that a habit and structure so exquisitely developed from a crude beginning and so nicely correlated with increasing complexity of social organization is without adaptive significance—in other words that the stridulatory notes go unperceived, although for reasons already presented and others to be given it seems unlikely that they are sensed as aerial vibrations.

Confirmatory to the supposition that the stridulatory vibrations are perceived mechanically is the absence of the organ in many genera living largely in the open air, where, supposedly, perception of the oscillations through material media would become increasingly difficult. Closely resemblant as the *Dorylinae* are to the *Ponerinae* in many respects, it is indeed surprising that in none of them is a true stridulatory organ developed, as Sharp and Wheeler have found. The polygonal asperites of the first and second peduncular nodes are in most cases wholly unspecialized. In such ants as the Drivers the existence of a means of sound-production would seem especially valuable, and it is possible that its total absence may be explainable on the ground of its comparative uselessness in the habitually more open conditions amid which the *Dorylinae* spend the greater part of their lives.

An equally striking case is that of the genus *Cryptocerus*, in which, as shown by Sharp, the stridulatory file is totally absent, although the *Cryptocerii* are a tribe of the *Myrmicinae*, and the beautiful specialization of the chitinous investment in other directions would certainly lead the investigator to hazard its existence. The writer has found the file to be similarly absent in the allied genus *Cephalates*, and it is believed that the same condition will be found throughout the *Cryptocerii*. The genera *Cryptocerus* and *Cephalates* are both composed of tropical ants almost wholly arboreal in habit.

The absence of the stridulatory organ throughout the *Dolichoderinae* and *Formicinae* is not so readily explainable, and is probably the result of the action of a much more complex set of conditions. For although it is probably true that a larger percentage of ants in those subfamilies are of arboreal or pronouncedly epigaeic habit than elsewhere, it is equally true that no degenerative development from primitive earth-dwelling types can be traced. There is no more trace of the file in primitive or hypogaeic Formicines than in arboreal forms, and it is difficult to believe that the structure was ever present in this subfamily. It is interesting to notice, however, that in those Formicines which, as Forbes (1881) and Peal (1881) have shown for *Polyrhacis* and as has been amply confirmed by other observers, employ supplementary means of sound-production, these are always, so far as known, of a percussion type, such as the striking of a hard and resonant surface with the head or gaster—actions which would set up vibrations of the medium capable of transmission for some distance.

There is one serious objection to the supposition that stridulatory noises are normally sensed mechanically. This is the assumption which is commonly made that the sounds given out by the stridulatory action of ants are of extremely high pitch. It is of course evident in audibly stridulating types that the sound is of relatively low pitch, but this has been considered not to be the case with smaller, inaudibly stridulating species, especially among the *Myrmicinae*. If the sounds emitted by such species were actually far above the humanly audible range, there would be serious question of whether they would be capable of forcing vibrations of sufficient magnitude to be mechanically perceived in fairly massive media, even by the extremely delicate tactile sense of ants. It is the purpose of the remaining portion of this paper to present the results of certain tests which suggest that the inaudibility of the stridulatory note of small ants is due, not to its very high pitch, but purely to lack of sufficient volume to induce oscillations in the human tympanum.

The extreme specialization of the anterior portion of the abdomen in the *Myrmicinae* permits of such freedom of motion in stridulation that the action is readily perceptible in most cases. It is undoubtedly true that, because of the delicate adjustment of the inturned scraper on the segment preceding that carrying the file of which all stridulating ants are capable, it is possible for Myrmicine ants to produce some sound when only a very small portion of the file is used, and when such a motion cannot be visually detected. Under such a stimulus as fear, however, stridulation is very vigorous, and the amplitude of motion is invariably, so far as has been observed, such as to bring the whole file into play and to be readily seen.

It was believed that advantage might be taken of this situation to arrive at a rough determination of the pitch of the sound emitted by certain small Myrmicines. Knowing the number of teeth in the file and the rapidity with which they are crossed by the scraper, the calculation of the pitch is of course extremely simple, being further simplified by the assurance that the whole file is covered in the motion and by the fact that the scraper takes the form, in all ants possessing it, of a thin, resonant, highly chitinized blade. The difficulties of the method lie in the tremendous field which it opens for observational errors in estimating the number of teeth in the file and especially in counting the gastric strokes in stridulation. The rate of gastric motion, while by no means too great to be followed, is yet sufficiently high to make accurate counting by a simple ocular method somewhat difficult. To minimize this latter error, 1000 separate tests were made on four species of small Myrmicine ants—*Myrmica scabrinodis sabuleti*, *Aphaenogaster fulva aquia*, *Leptothorax longispinosus*, and *Solenopsis molesta*, and for each species a general average of the 250 tests made on it was obtained.

The simple method used was briefly as follows. The ant in question was fastened by the head and fore portion of the thorax to a microscope slide, so that a lateral view was obtained, and the pedicel and gaster were unrestricted in motion. This portion of the insect was then viewed through a microscope, a power of 37.5 diameters proving most convenient. The excitement of its unusual situation was sufficient, as a rule, to stimulate the imprisoned ant to constant stridulation for several minutes, during which groups of strokes, intentionally varied in number, were timed with a split-second stop watch and recorded as shown in the following tables. It proved a considerable help in increasing accuracy to count as one stroke a complete cycle, involving two strokes of the scraper and file, and the

motion has been so recorded. A doubling of the number given under *Strokes* is necessary to obtain the true value. The fatigue-curve varied considerably in different species, but was so steep in the last three tested that after three or four minutes spontaneous stridulation no longer occurred. The stimulus then used was a small stream of air directed at the head of the ant. This was effective for several additional minutes, but it was necessary to change individuals frequently, as the efficacy of the air-blast diminished.

The case of *Myrmica scabrinodis* was much more interesting, and may well be considered separately. The 231 tests first recorded were made on a single individual, and furnish remarkable evidence of the wonderful power of sustained stridulation developed in certain of the *Myrmicinae*. A graph (D, page 134) of the performance of this individual, plotted as strokes/min. $\times 10^{-2}$ against stroke-number in ten-stroke intervals follows the tables, to show the effect of advancing fatigue.

TABLE III

RATE OF GASTRIC MOTION IN STRIDULATION OF *Myrmica scabrinodis sabuleti*

Trial	Strokes	Min./100	Rate	Trial	Strokes	Min./100	Rate
1	27	8 0	3 4	32	114	22 0	5 2
2	53	14 0	3 8	33	150	41 3	3 6
3	102	23 0	4 4	34	41	10 0	4 1
4	62	12 5	5 0	35	84	21 6	3 9
5	53	10 0	5 3	36	70	16 6	4 2
6	22	5 0	4 4	37	70	18 0	3 9
7	100	20 0	5 0	38	105	24 3	4 3
8	61	14 0	4 4	39	290	70 3	4 1
9	120	21 3	5 6	40	83	20 3	4 1
10	76	14 0	5 4	41	57	15 3	3 7
11	66	14 0	4 7	42	226	65 6	3 5
12	100	18 0	5 6	43	75	20 6	3 6
13	40	10 6	3 8	44	100	26 0	3 9
14	130	29 0	4 5	45	38	11 0	3 5
15	100	29 3	3 4	46	67	19 3	3 5
16	100	18 6	5 4	47	390	133 6	2 9
17	70	15 3	4 6	48	207	54 0	3 8
18	45	11 3	4 0	49	22	7 3	3 0
19	91	17 0	5 4	50	72	18 0	4 0
20	150	33 0	4 5	51	42	9 0	4 7
21	120	35 0	3 4	52	61	15 0	4 1
22	100	25 3	4 0	53	78	17 6	4 4
23	98	25 0	3 9	54	41	9 0	4 6
24	24	6 6	3 6	55	46	12 3	3 8
25	19	8 0	2 4	56	51	13 6	3 8
26	52	15 6	3 3	57	35	9 0	3 9
27	35	25 6	1 4	58	40	9 6	4 2
28	62	13 0	4 8	59	75	14 0	5 4
29	109	21 3	5 1	60	151	35 0	4 3
30	140	26 3	5 3	61	11	5 0	2 2
31	220	47 3	4 6	62	67	13 0	5 2

Trial	Strokes	Min./100	Rate	Trial	Strokes	Min./100	Rate
63	84	21.6	3.9	122	5	2.3	2.2
64	78	21.3	3.7	123	72	15.6	4.6
65	165	40.0	4.2	124	12	4.0	3.0
66	275	72.6	3.8	125	40	10.0	4.0
67	352	88.3	4.0	126	40	9.3	4.3
68	258	61.6	4.2	127	60	11.0	5.5
69	165	35.0	4.7	128	98	25.0	3.9
70	189	39.6	4.8	129	49	8.3	5.9
71	29	10.6	2.7	130	97	21.0	4.6
72	72	14.6	4.9	131	53	13.6	3.9
73	80	15.3	5.2	132	40	9.6	4.2
74	58	14.0	4.1	133	33	11.0	3.0
75	55	14.0	3.9	134	57	17.0	3.4
76	72	16.6	4.3	135	111	31.0	3.6
77	45	11.0	4.1	136	8	2.6	3.1
78	57	13.3	4.3	137	99	19.3	5.1
79	52	12.3	4.3	138	100	16.0	6.3
80	114	24.3	4.7	139	111	21.0	5.3
81	207	45.3	4.6	140	173	37.6	4.6
82	51	10.6	4.8	141	16	5.6	2.9
83	72	13.3	5.4	142	37	9.3	4.0
84	91	18.6	4.9	143	45	16.9	2.7
85	92	20.3	4.6	144	164	45.0	3.6
86	281	59.6	4.7	145	146	38.6	3.8
87	44	10.0	4.4	146	82	21.0	3.9
88	426	112.6	3.8	147	76	22.3	3.4
89	45	12.0	3.8	148	40	12.3	3.3
90	72	14.0	5.2	149	85	21.3	4.0
91	25	7.6	3.3	150	40	16.3	2.5
92	43	10.9	3.9	151	33	13.0	2.5
93	77	15.6	4.9	152	45	25.3	1.8
94	48	12.3	3.9	153	131	33.6	3.9
95	50	12.3	4.1	154	130	35.6	3.7
96	90	18.6	4.8	155	145	44.3	3.3
97	79	14.6	5.4	156	30	10.0	3.0
98	57	14.0	4.1	157	431	104.6	4.1
99	77	18.0	4.3	158	62	14.6	4.2
100	25	6.6	3.8	159	45	13.0	3.5
101	85	19.0	4.5	160	21	7.0	3.0
102	60	15.0	4.0	161	24	8.3	2.9
103	49	12.0	4.1	162	70	18.3	3.8
104	66	16.0	4.1	163	26	15.6	1.7
105	73	16.6	4.4	164	27	7.6	3.6
106	64	13.3	4.8	165	30	11.9	2.5
107	53	11.0	4.8	166	31	12.3	2.5
108	12	4.3	2.8	167	5	3.6	1.4
109	40	7.6	5.3	168	40	16.0	2.5
110	88	37.3	2.3	169	52	12.0	4.3
111	79	47.3	1.7	170	12	4.0	3.0
112	120	53.0	2.3	171	42	12.6	3.3
113	108	20.0	5.4	172	56	19.0	2.9
114	60	15.6	3.9	173	34	11.0	3.1
115	137	28.0	4.9	174	63	14.3	4.4
116	260	45.3	5.7	175	35	10.0	3.5
117	86	14.3	6.0	176	13	5.3	2.5
118	75	15.0	5.0	177	70	21.3	3.3
119	120	23.0	5.2	178	11	3.3	3.3
120	71	14.0	5.1	179	78	18.3	4.3
121	43	13.0	3.3	180	20	5.3	3.8

Trial	Strokes	Min./100	Rate	Trial	Strokes	Min./100	Rate
181	10	3.3	3.0	207	12	3.0	4.0
182	10	2.6	3.8	208	3	2.0	1.5
183	12	3.3	3.6	209	10	3.6	2.8
184	11	2.6	4.2	210	7	2.6	2.7
185	19	5.3	3.6	211	24	7.3	3.3
186	50	13.0	3.8	212	8	2.3	3.5
187	16	4.6	3.5	213	15	6.0	2.5
188	14	4.3	3.3	214	12	4.0	3.0
189	19	6.0	3.2	215	15	4.3	3.5
190	51	15.6	3.3	216	12	3.0	4.0
191	6	2.0	3.0	217	10	4.0	2.5
192	17	5.0	3.4	218	5	2.0	2.5
193	12	4.0	3.0	219	12	3.6	3.3
194	5	2.6	1.9	220	26	7.6	3.4
195	4	2.6	1.5	221	12	3.0	4.0
196	10	3.6	2.8	222	11	4.3	2.6
197	22	7.0	3.1	223	22	5.6	3.9
198	7	2.6	2.7	224	7	2.6	2.7
199	12	3.0	4.0	225	12	4.0	3.0
200	6	3.0	2.0	226	12	3.3	3.6
201	12	4.0	3.0	227	15	5.3	2.8
202	20	6.6	3.0	228	8	2.3	3.5
203	5	2.0	2.5	229	7	3.3	2.1
204	14	4.3	3.3	230	7	2.3	3.0
205	20	5.0	4.0	231	7	3.3	2.1
206	21	6.0	3.5				

TABLE IV

RATE OF GASTRIC MOTION IN STRIDULATION OF *Aphaenogaster fulva aquia*

Trial	Strokes	Min./100	Rate	Trial	Strokes	Min./100	Rate
1	94	28.6	3.3	27	52	12.0	4.3
2	165	47.3	3.5	28	20	5.3	3.8
3	12	4.0	3.0	29	41	8.3	4.9
4	62	15.0	4.1	30	12	3.3	3.6
5	73	37.0	2.0	31	31	5.6	5.5
6	91	17.0	5.4	32	33	6.0	5.5
7	192	47.6	4.0	33	21	5.0	4.2
8	76	22.0	3.5	34	30	5.6	5.4
9	13	4.3	3.0	35	17	4.0	4.3
10	10	4.0	2.5	36	14	3.3	4.2
11	8	2.6	3.1	37	34	7.6	4.5
12	12	3.6	3.3	38	6	2.3	2.6
13	11	3.3	3.3	39	25	7.0	3.6
14	84	18.3	4.6	40	23	5.0	4.6
15	72	12.3	5.9	41	32	8.3	3.9
16	170	31.6	5.4	42	34	8.3	4.1
17	51	10.0	5.1	43	24	5.6	4.3
18	42	8.0	5.3	44	34	8.0	4.3
19	33	6.6	5.0	45	25	7.0	3.6
20	86	20.0	4.3	46	35	9.3	3.8
21	11	3.3	3.3	47	21	5.0	4.2
22	52	15.0	3.5	48	33	9.0	3.7
23	34	8.3	4.1	49	34	8.0	4.3
24	23	7.3	3.2	50	43	11.3	3.8
25	44	13.0	3.4	51	22	8.3	2.7
26	33	10.0	3.3	52	33	10.0	3.3

Trial	Strokes	Min./100	Rate
53	131	27.6	4.7
54	21	5.3	4.0
55	61	12.0	5.1
56	24	6.3	3.8
57	21	6.0	3.5
58	51	10.6	4.8
59	52	11.0	4.7
60	44	11.6	3.8
61	82	18.3	4.5
62	163	29.3	5.6
63	12	5.0	2.4
64	120	23.3	5.2
65	22	5.6	3.9
66	14	6.0	2.3
67	52	10.6	4.9
68	223	40.3	5.5
69	36	8.3	4.3
70	110	20.0	5.5
71	24	7.6	3.2
72	51	11.0	4.6
73	11	4.0	2.8
74	10	4.0	2.5
75	16	4.3	3.7
76	8	2.0	4.0
77	5	1.6	3.1
78	8	1.3	6.2
79	13	3.0	4.3
80	12	3.6	3.3
81	6	1.6	3.8
82	17	4.3	4.0
83	22	5.0	4.4
84	23	5.6	4.1
85	32	6.3	5.1
86	29	7.6	3.8
87	23	6.0	3.8
88	25	6.0	4.2
89	9	3.3	2.7
90	21	4.3	4.9
91	13	3.3	3.9
92	7	2.3	3.0
93	11	3.0	3.7
94	21	4.6	4.6
95	22	5.0	4.4
96	24	6.0	4.0
97	10	3.3	3.0
98	18	4.0	4.5
99	28	6.3	4.4
100	22	5.3	4.2
101	48	11.6	4.1
102	18	5.3	3.4
103	32	8.0	4.0
104	187	35.3	5.3
105	50	11.3	4.4
106	41	10.0	4.1
107	50	11.0	4.5
108	32	7.3	4.4
109	109	24.3	4.5
110	54	14.6	3.7
111	112	26.3	4.3
112	108	20.0	5.4
113	51	10.0	5.1
114	232	77.3	3.0
115	35	14.3	2.4
116	20	8.3	2.4
117	30	14.6	2.1
118	12	4.0	3.0
119	52	13.0	4.0
120	34	7.3	4.7
121	40	9.6	4.2
122	40	11.0	3.6
123	43	10.0	4.3
124	71	14.0	5.1
125	47	11.0	4.3
126	62	14.0	4.4
127	107	23.0	4.7
128	95	20.3	4.7
129	26	7.3	3.6
130	23	7.0	3.3
131	104	29.3	3.5
132	63	11.3	5.6
133	26	6.6	3.9
134	99	18.0	5.5
135	18	5.3	3.4
136	23	6.0	3.8
137	9	3.0	3.0
138	72	16.3	4.4
139	22	9.0	2.4
140	46	13.0	3.5
141	18	6.3	2.9
142	8	2.6	3.1
143	4	1.6	2.5
144	33	8.6	3.8
145	11	4.0	2.8
146	50	16.0	3.1
147	60	14.0	4.3
148	7	3.3	2.2
149	13	4.0	3.3
150	93	20.0	4.6
151	9	4.0	2.3
152	7	4.0	1.8
153	6	1.3	4.6
154	20	6.0	3.3
155	7	2.6	2.7
156	10	3.0	3.3
157	24	8.0	3.0
158	23	4.3	5.3
159	16	2.6	6.2
160	11	1.6	6.9
161	17	2.3	7.4
162	17	5.0	3.4
163	10	2.6	3.8
164	20	5.3	3.8
165	15	4.0	3.8
166	9	4.3	2.1
167	11	5.0	2.2
168	40	11.0	3.6
169	18	5.6	3.2
170	15	5.0	3.0

Trial	Strokes	Min./100	Rate	Trial	Strokes	Min./100	Rate
171	12	3.3	3.6	211	25	6.3	4.0
172	32	8.6	3.7	212	22	5.3	4.2
173	120	36.6	3.3	213	15	4.0	3.8
174	16	5 6	2.9	214	52	10.3	5.0
175	507	111.6	4.5	215	41	8.3	4.9
176	45	14 0	3.2	216	14	2.6	5.4
177	118	24.6	4 8	217	62	10.0	6.2
178	105	20 3	5 2	218	13	3.6	3.6
179	31	8 6	3 6	219	34	7.6	4.5
180	51	10.6	4 8	220	42	7.6	5.5
181	16	5 0	3.2	221	14	3.0	4.7
182	109	26.6	4.1	222	41	7.3	5.6
183	71	17.6	4.0	223	40	15.3	2.6
184	41	12.0	3.4	224	27	7.6	3.6
185	11	3.3	3 3	225	52	9.6	5.4
186	42	10.0	4.2	226	29	9.6	3.0
187	101	19.0	5.3	227	92	17.6	5.2
188	23	6.3	3.7	228	32	7.3	4.4
189	20	6.0	3.3	229	53	11.0	4.8
190	51	10.0	5.1	230	74	15.0	4.9
191	34	6.0	5.7	231	40	8.6	4.7
192	32	7 3	4.4	232	32	6.3	5.1
193	83	15.0	5.5	233	100	19.6	5.1
194	18	5.0	3.6	234	34	11.6	2.9
195	92	15.3	6.0	235	74	14.0	5.3
196	6	1.6	3 8	236	40	7.6	5.3
197	10	3.0	3.3	237	22	8.0	2.8
198	4	2 0	2.0	238	40	6.6	6.1
199	241	49.0	4.9	239	190	35.3	5.4
200	200	36.3	5.5	240	21	4 6	4.6
201	12	3 3	3.6	241	22	5.0	4.4
202	10	3 3	3.0	242	61	11.3	5.4
203	172	34.6	5.0	243	34	7.6	4 5
204	51	10.0	5.1	244	14	5.0	2.8
205	5	1.6	3 1	245	153	29.0	5 3
206	32	7 3	4.4	246	31	7.6	4.1
207	103	18.6	5.5	247	26	5.6	4.6
208	31	6.0	5.2	248	21	3.6	5.8
209	6	2 3	2.6	249	17	3 3	5 2
210	73	15.6	4.7	250	16	2.3	7.0

TABLE V

RATE OF GASTRIC MOTION IN STRIDULATION OF *Leptothorax longispinosus*

Trial	Strokes	Min./100	Rate	Trial	Strokes	Min./100	Rate
1	36	12.0	3.0	14	16	3.3	4.8
2	35	14.0	2.5	15	15	2.0	7 5
3	14	2.6	5.4	16	15	2 3	6.5
4	16	4.0	4.0	17	16	4.0	4.0
5	15	3.0	5.0	18	20	4.3	4 7
6	15	3.0	5.0	19	16	3.6	4.4
7	20	4.3	4.7	20	15	3.0	5.0
8	18	4.3	4.2	21	15	3.3	4.5
9	17	3.3	5.2	22	15	3.0	5.0
10	15	3.0	5.0	23	15	2.3	6.5
11	15	2.6	5.8	24	15	2.6	5.8
12	14	3.0	4.7	25	15	2.6	5.8
13	15	2 6	5.8	26	16	2.3	7.0

Trial	Strokes	Min./100	Rate	Trial	Strokes	Min./100	Rate
27	12	2.3	5.2	83	10	2 0	5.0
28	13	2.3	5.7	84	5	1.0	5.0
29	9	1.3	6.9	85	9	1 3	6.9
30	13	2.0	6.5	86	6	1 0	6.0
31	7	1.3	5.4	87	17	2 6	6 5
32	15	2.3	6.5	88	10	1.3	7.7
33	14	3.3	4.2	89	13	2.0	6.5
34	14	2.6	5.4	90	13	2.3	5 7
35	15	2.6	5.8	91	5	0 6	8.3
36	15	2.3	6.5	92	5	1 0	5.0
37	15	2.6	5.8	93	12	1 3	9 2
38	15	3.0	5.0	94	10	2.0	5 0
39	15	2.3	6.5	95	10	1.6	6 3
40	21	3.3	6.4	96	10	1 3	7.7
41	26	6.6	3.9	97	11	1.6	6.9
42	18	3.3	5.5	98	13	1.0	13 0
43	20	3.3	6.1	99	7	1.6	4.4
44	18	3.6	5.0	100	7	1.3	5.4
45	20	3.6	5.6	101	7	1.6	4.4
46	15	2.6	5.8	102	3	0.6	5.0
47	15	2.3	6.5	103	10	1 3	7.7
48	20	4.0	5.0	104	3	0.3	10.0
49	13	2.0	6.5	105	8	1.3	6 2
50	14	2.3	6.1	106	10	1 6	6.3
51	17	3.0	5.7	107	6	1.0	6.0
52	10	1.6	6.3	108	6	1 3	4 6
53	14	3.6	3.9	109	5	1 3	3.9
54	13	2.0	6.5	110	8	1.0	8.0
55	14	2.6	5.4	111	9	1 6	5 6
56	15	2.0	7.5	112	5	0 6	8.3
57	15	3.3	4.5	113	3	0.6	5.0
58	10	2.0	5.0	114	5	1 0	5.0
59	17	3.0	5.7	115	8	1.6	5.0
60	15	3.0	5.0	116	11	3.6	3.1
61	12	2.6	4.6	117	6	1.0	6.0
62	11	2.6	4.2	118	10	1.3	7.7
63	10	3.3	3.0	119	10	1.6	6.3
64	11	2.6	4.2	120	5	1.0	5 0
65	11	2.3	4.8	121	7	1.0	7.0
66	12	2.3	5.2	122	9	0 6	15.0
67	11	2.0	5.5	123	7	1.0	7.0
68	15	3.0	5.0	124	11	1.0	11.0
69	12	2.3	5.2	125	11	1.6	6.9
70	11	2.6	4.2	126	17	3.6	4.7
71	9	1.3	6.9	127	17	2.6	6.5
72	9	1.3	6.9	128	11	1.3	8.5
73	9	2.3	3.9	129	10	2.0	5 0
74	8	1.3	6.2	130	7	1.0	7.0
75	15	2.0	7.5	131	10	1.0	10.0
76	15	2.6	5.8	132	10	1.0	10.0
77	5	1.6	3.1	133	11	1.0	11.0
78	8	1.6	5.0	134	10	1.3	7.7
79	6	1.3	4.6	135	14	2.0	7.0
80	9	2.3	3.9	136	13	1.3	10 0
81	10	2.0	5.0	137	7	2.0	3.5
82	7	1.3	5.4	138	10	1.3	7.7

Trial	Strokes	Min./100	Rate	Trial	Strokes	Min./100	Rate
139	11	1.6	6.9	195	11	2.6	4.2
140	10	1.3	7.7	196	10	1.6	6.3
141	7	1.0	7.0	197	11	2.6	4.2
142	8	1.6	5.0	198	11	2.0	5.5
143	7	0.6	11.7	199	7	2.0	3.5
144	8	1.3	6.2	200	13	2.0	6.5
145	5	1.0	5.0	201	11	2.0	5.5
146	7	0.6	11.7	202	15	2.3	6.5
147	4	0.6	6.7	203	14	2.6	5.4
148	11	2.6	4.2	204	17	2.6	6.5
149	6	0.6	10.0	205	15	2.0	7.5
150	7	0.6	11.7	206	17	2.3	7.4
151	9	1.0	9.0	207	10	2.0	5.0
152	8	1.6	5.0	208	13	2.0	6.5
153	7	1.0	7.0	209	15	2.3	6.5
154	7	1.0	7.0	210	15	2.3	6.5
155	8	1.3	6.2	211	26	6.0	4.3
156	13	1.3	10.0	212	6	2.0	3.0
157	10	2.0	5.0	213	10	2.0	5.0
158	8	1.6	5.0	214	13	3.0	4.3
159	5	0.6	8.3	215	15	2.6	5.8
160	10	3.0	3.3	216	17	2.6	6.5
161	7	1.0	7.0	217	14	2.3	6.1
162	7	1.6	4.4	218	17	2.6	6.5
163	11	2.0	5.5	219	15	2.0	7.5
164	10	1.3	7.7	220	7	1.6	4.4
165	11	2.0	5.5	221	7	0.6	11.7
166	10	1.6	6.3	222	15	3.0	5.0
167	10	1.0	10.0	223	11	3.3	3.3
168	10	1.6	6.3	224	11	2.0	5.5
169	13	1.6	8.1	225	8	1.3	6.2
170	16	2.6	6.2	226	7	1.6	4.4
171	15	2.0	7.5	227	13	1.6	8.1
172	11	1.3	8.5	228	13	2.6	5.0
173	12	1.3	9.2	229	12	3.0	4.0
174	11	1.3	8.5	230	7	2.6	2.7
175	12	1.6	7.5	231	10	2.3	4.3
176	7	1.0	7.0	232	13	2.0	6.5
177	11	2.0	5.5	233	11	2.6	4.2
178	12	2.3	5.2	234	16	2.6	6.2
179	11	2.0	5.5	235	13	2.3	5.7
180	11	3.3	3.3	236	15	3.3	4.5
181	11	2.0	5.5	237	12	1.6	7.5
182	11	2.3	4.8	238	7	1.6	4.4
183	11	1.3	8.5	239	4	0.6	6.7
184	11	1.6	6.9	240	10	1.6	6.3
185	7	1.6	4.4	241	11	2.3	4.8
186	11	1.3	8.5	242	11	2.0	5.5
187	13	3.0	4.3	243	11	2.0	5.5
188	11	2.0	5.5	244	5	1.0	5.0
189	11	2.0	5.5	245	12	2.0	6.0
190	12	3.0	4.0	246	12	2.0	6.0
191	15	2.3	6.5	247	10	2.0	5.0
192	11	2.6	4.2	248	9	2.0	4.5
193	15	2.6	5.8	249	11	3.0	3.7
194	17	2.6	6.5	250	14	3.0	4.7

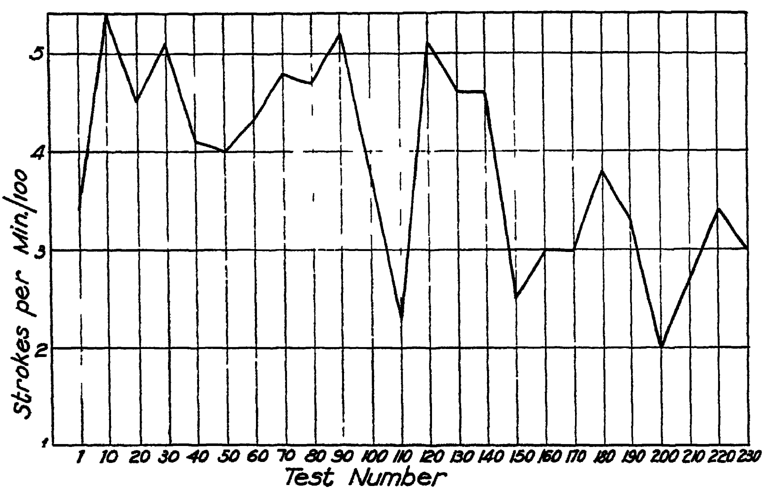
TABLE VI

RATE OF GASTRIC MOTION IN STRIDULATION OF *Solenopsis molesta*

Trial	Strokes	Min./100	Rate	Trial	Strokes	Min./100	Rate
1	8	2.0	4.0	51	14	3.0	4.7
2	60	10.6	5.7	52	5	1.6	3.1
3	10	2.3	4.3	53	7	1.3	5.4
4	13	4.0	3.3	54	8	1.6	5.0
5	11	3.3	3.3	55	8	2.0	4.0
6	15	3.3	4.5	56	8	2.0	4.0
7	15	3.6	4.2	57	11	3.3	3.3
8	16	3.0	5.3	58	5	1.6	3.1
9	15	3.3	4.5	59	2	1.0	2.0
10	16	4.6	3.5	60	12	3.3	3.6
11	12	3.0	4.0	61	13	3.0	4.3
12	15	2.3	6.5	62	12	3.6	3.3
13	15	2.6	5.8	63	5	2.3	2.2
14	9	2.0	4.5	64	13	3.0	4.3
15	15	2.6	5.8	65	12	3.6	3.3
16	11	2.3	4.8	66	10	3.3	3.0
17	7	1.6	4.4	67	11	3.3	3.3
18	14	2.3	6 1	68	11	3.6	3.1
19	11	2.3	4 8	69	4	1.6	2.5
20	7	2.0	3.5	70	9	2.6	3.5
21	11	2.3	4.8	71	13	2.6	5.0
22	11	2.3	4.8	72	8	2.0	4.0
23	13	3.0	4.3	73	7	3.3	2.1
24	15	2.3	6.5	74	14	4.3	3.3
25	15	3.0	5 0	75	8	3.0	2.7
26	13	2 6	5.0	76	20	5.0	4.0
27	16	2.6	6.2	77	14	3.3	4.2
28	13	2.6	5.0	78	5	1.3	3.8
29	16	2.6	6.2	79	5	1.6	3.1
30	11	2.0	5.5	80	5	0.6	8.3
31	13	2.3	5.7	81	13	2.3	5.7
32	13	2.6	5.0	82	12	2.6	4.6
33	17	4.3	4.0	83	5	1.6	3.1
34	12	3.0	4.0	84	14	3.6	3.9
35	11	3.0	3.7	85	5	2.3	2.2
36	10	2.3	4.3	86	8	3.0	2.7
37	11	2.0	5.5	87	9	3.6	2.5
38	10	2.6	3.8	88	20	4.0	5.0
39	11	2.6	4 2	89	20	3.0	6.7
40	13	2.3	5.7	90	50	9.3	5.4
41	13	2.6	5.0	91	25	4.3	5.8
42	12	3.6	3.3	92	22	4.3	5.1
43	13	2.3	5 7	93	30	6.0	5.0
44	11	3.0	3.7	94	22	4.0	5 5
45	9	2.0	4.5	95	14	3.3	4.2
46	12	2.6	4.6	96	15	2.3	6.5
47	7	1.6	4.4	97	20	5.0	4.0
48	16	3.3	4.8	98	17	4.0	4.3
49	9	2.3	3.9	99	8	2.0	4.0
50	11	3.0	3.7	100	20	4.6	4.3

Trial	Strokes	Min./100	Rate	Trial	Strokes	Min./100	Rate
101	18	3.0	6.0	157	11	1.3	8.5
102	15	3.3	4.5	158	5	1.0	5.0
103	18	3.0	6.0	159	5	0.6	8.3
104	20	5.0	4.0	160	8	2.6	3.1
105	20	4.0	5.0	161	5	1.3	3.8
106	20	4.0	5.0	162	8	1.3	6.2
107	28	6.3	4.4	163	11	1.6	6.9
108	15	3.0	5.0	164	12	2.3	5.2
109	17	4.3	4.0	165	7	1.6	4.4
110	17	4.0	4.3	166	5	1.0	5.0
111	26	6.3	4.1	167	7	1.0	7.0
112	20	4.6	4.3	168	15	2.0	7.5
113	22	4.0	5.5	169	15	2.0	7.5
114	6	1.3	4.6	170	5	1.3	3.8
115	8	2.0	4.0	171	8	2.3	3.5
116	20	4.0	5.0	172	11	2.0	5.5
117	15	3.3	4.5	173	5	1.3	3.8
118	16	3.0	5.3	174	11	3.0	3.7
119	15	3.0	5.0	175	11	1.6	6.9
120	16	3.0	5.3	176	13	3.0	4.3
121	21	4.3	4.9	177	12	2.0	6.0
122	16	4.0	4.0	178	9	1.3	6.9
123	16	3.6	4.4	179	11	2.0	5.5
124	12	3.0	4.0	180	15	2.6	5.8
125	12	2.6	4.6	181	16	2.6	6.2
126	13	2.3	5.7	182	11	2.0	5.5
127	11	3.3	3.3	183	12	1.6	7.5
128	24	4.3	5.6	184	15	2.6	5.8
129	16	3.0	5.3	185	17	2.6	6.5
130	16	3.0	5.3	186	12	1.6	7.5
131	16	4.0	4.0	187	8	2.0	4.0
132	20	4.3	4.7	188	18	4.0	4.5
133	5	1.3	3.8	189	18	3.0	6.0
134	13	2.0	6.5	190	22	5.3	4.2
135	14	2.3	6.1	191	10	2.0	5.0
136	4	1.6	2.5	192	20	4.0	5.0
137	16	3.6	4.4	193	12	2.6	4.6
138	6	1.6	3.8	194	15	3.0	5.0
139	11	2.0	5.5	195	30	5.3	5.7
140	4	1.3	3.1	196	35	7.3	4.8
141	8	1.6	5.0	197	22	4.0	5.5
142	11	2.0	5.5	198	20	4.0	5.0
143	13	2.6	5.0	199	44	8.3	5.3
144	11	2.0	5.5	200	43	8.0	5.4
145	16	2.3	7.0	201	15	3.0	5.0
146	12	2.0	6.0	202	12	2.0	6.0
147	7	2.0	3.5	203	20	4.6	4.3
148	12	2.6	4 6	204	24	4.6	5 2
149	7	1.3	5.4	205	13	2.3	5.7
150	11	2.6	4.2	206	15	2.3	6.5
151	5	1.3	3.8	207	15	3.3	4.5
152	6	1.6	3.8	208	20	3.0	6.7
153	6	1.0	6.0	209	21	3.3	6.4
154	10	2.0	5.0	210	12	2.3	5.2
155	11	2.3	4.8	211	16	2.6	6.2
156	9	1.3	6.9	212	22	4.3	5.1

Trial	Strokes	Min./100	Rate	Trial	Strokes	Min./100	Ra
213	11	4.3	2.5	232	24	5.6	4.
214	17	3.3	5.2	233	15	3.0	5.
215	25	5 0	5.0	234	22	4.6	4.
216	16	2.6	6.2	235	23	4.3	5.
217	16	3.0	5.3	236	27	6.0	4.
218	23	6 0	3.8	237	28	6.0	4.
219	16	4.3	3.7	238	25	5.3	4.
220	16	5.0	3.2	239	18	5.3	3.
221	17	5.0	3.4	240	17	4.6	3.
222	15	4.0	3.8	241	11	4.6	2.
223	15	3.3	4.5	242	20	4.3	4.
224	11	3.3	3.3	243	23	5.3	4.
225	14	3 3	4.2	244	19	4 3	4.
226	17	3.6	4.7	245	22	5.6	3.
227	16	4.3	3.7	246	10	3.3	3.
228	10	3.3	3.0	247	20	6.0	3.
229	27	5 3	5.1	248	7	2 6	2.
230	15	5 0	3.0	249	15	4.0	3.
231	21	5.3	4.0	250	15	4.0	3.

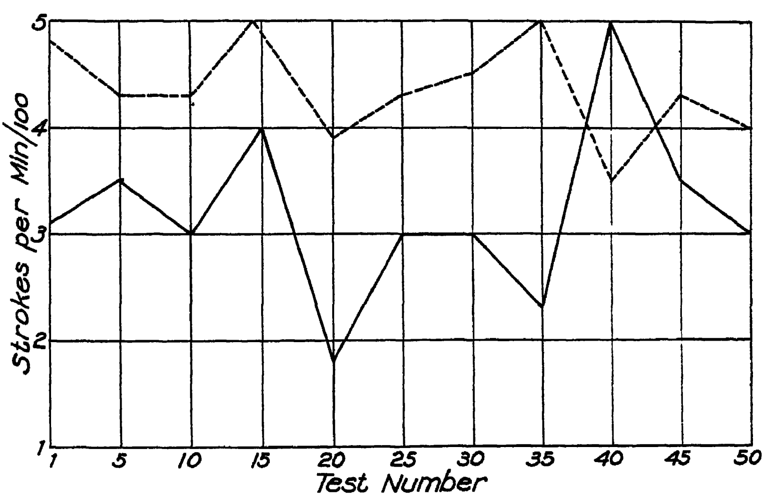


GRAPH D. Rate of gastric motion in stridulation of *Myrmica scabrinodis sabuleti*. (See page 125.)

Janet's estimate of the number of teeth in the file of *Myrmica rubra* (1894a) limits that number between 100 and 150, with 138 as the best value. It is in all probability variant in different individuals. The estimate of the present writer for *M. scabrinodis sabuleti* lies between 100 and 150, with 120 as the best value. The general average of the 231 recorded tests on this insect presented above yields a rate of 3.9 strokes per hundredth of a minute as counted, an actual rate of 7.8 complete traverses of the file by the scraper per hundredth of a minute, or 13.0 per second. This would produce a note, on Janet's

estimate for the number of teeth for *M. rubra*, of a frequency of 1,794/sec., or on the writer's estimate for the variety tested, of 1,560/sec. Both pitches are far within the limit of human audibility, and are by no means high enough to cast doubt on the supposition that they may produce forced vibrations of some amplitude in suitable material media.

It was quite noticeable, however, that the frequency-curve for a single stridulatory series rose very rapidly during the first ten to fifteen strokes, and thereafter remained nearly level throughout the call. The present average, of course, carried these first slower strokes, and it was thought that the later ones would, if isolated, show a higher average frequency. To make certain that this factor did not invalidate the conclusion given, fresh individuals were used, and the first strokes, between 1 and 11, timed separately for fifty tests, while another series, also of fifty trials, was run timing strokes beyond the tenth. Results were obtained as shown on the following page. The results obtained in timing the first ten strokes are comprised in the left hand column, those in timing later strokes in the right. A graph follows, showing these results again plotted as strokes/min. $\times$ 10^{-2}, but in this case against trial number for several trials, the early strokes being represented by the full, the later by the broken, line.



GRAPH E.

TABLE VII

Trial	Strokes	Min./100	Rate	Trial	Strokes	Min./100	Rate
1	5	1.6	3.1	1	16	3.3	4.8
2	6	2.0	3.0	2	12	3.0	4.0
3	11	3.0	3.7	3	10	2.6	3.8
4	6	2.6	2.3	4	14	2.0	7.0
5	8	2.3	3.5	5	13	3.0	4.3
6	6	1.6	3.8	6	14	3.0	4.7
7	6	2.0	3.0	7	17	4.0	4.3
8	8	2.3	3.5	8	15	3.0	5.0
9	6	1.3	4.6	9	15	3.0	5.0
10	7	2.3	3.0	10	10	2.3	4.3
11	6	2.0	3.0	11	12	3.0	4.0
12	10	2.6	3.8	12	14	3.0	4.7
13	7	2.0	3.5	13	23	6.0	3.8
14	11	3.0	3.7	14	10	2.6	3.8
15	8	2.0	4.0	15	13	2.6	5.0
16	8	2.3	3.5	16	15	3.3	4.5
17	11	2.6	4.2	17	15	3.0	5.0
18	7	2.3	3.0	18	15	3.0	5.0
19	6	1.6	3.8	19	14	4.0	3.5
20	7	4.0	1.8	20	13	3.3	3.9
21	7	2.0	3.5	21	11	4.0	2.8
22	8	2.0	4.0	22	11	3.6	3.1
23	5	1.3	3.8	23	11	3.3	3.3
24	4	1.3	3.1	24	11	3.3	3.3
25	7	2.3	3.0	25	10	2.3	4.3
26	7	2.0	3.5	26	14	3.0	4.7
27	4	3.0	1.3	27	11	2.6	4.2
28	5	1.6	3.1	28	10	2.3	4.3
29	5	2.0	2.5	29	13	3.3	3.9
30	6	2.0	3.0	30	15	3.3	4.5
31	8	1.6	5.0	31	12	3.0	4.0
32	6	2.3	2.6	32	11	2.6	4.2
33	5	1.3	3.8	33	10	2.6	3.8
34	8	2.6	3.1	34	15	3.0	5.0
35	6	2.6	2.3	35	15	3.0	5.0
36	10	2.6	3.8	36	20	4.6	4.3
37	6	1.6	3.8	37	17	4.3	4.0
38	8	1.6	5.0	38	13	2.3	5.7
39	8	1.6	5.0	39	14	3.0	4.7
40	8	1.6	5.0	40	15	4.3	3.5
41	7	2.0	3.5	41	13	4.0	3.3
42	8	1.6	5.0	42	15	4.0	3.8
43	9	2.3	3.9	43	11	2.6	4.2
44	8	2.0	4.0	44	13	2.6	5.0
45	7	2.0	3.5	45	10	2.3	4.3
46	6	2.0	3.0	46	14	3.3	4.2
47	9	3.0	3.0	47	11	2.6	4.2
48	5	2.0	2.5	48	8	2.3	3.5
49	4	1.6	2.5	49	15	3.3	4.5
50	7	2.3	3.0	50	17	4.3	4.0

The average of the tests graphed as a broken line is a rate of 4.3 strokes per hundredth of a minute, that of those represented by a full line, 3.5, the average of the two being that of the previous 431 tests, and indicating quite clearly that the previous average was too low. The actual number of strokes per second at the height of the call was

more nearly 14.5, which would produce a note, on Janet's estimate of file-ridge number, of a frequency of 2001/sec.—still far within the humanly audible range. The highest single test recorded is that of Trial 4 in the series of tests after the tenth stroke. The recorded value here is 7.0, the actual value therefore 14/min. $\times$ 10^{-2}, or 23.3/sec., producing a note of 3215/sec. on Janet's estimate or 2796 on that of the writer. The lowest single rate recorded was that of Trial 27 of the series recording rates from the first to tenth strokes, it being observed as 1.3, actually 2.6/min. $\times$ 10^{-2}, or 4.3/sec. producing a sound of frequency 583.4/sec. Janet or 516/sec. by the writer's estimate.

It seems to the writer that these tests show rather conclusively that the stridulatory note ordinarily emitted by *M. scabrinodis sabuleti* is not only of sufficiently low frequency very readily to induce forced vibrations in the soil, but is far within the range of human audibility. Were the sound emitted to be of a frequency greater than 20,000/sec., approximately the lowest upper limit of normal human hearing, the observational error committed would necessarily have been many hundred per cent, which seems inconceivable.

It was found with the other three species tested that the rapid rise of the frequency of stridulation from the beginning of the call was not present. The rate instead was nearly consistent throughout. Curiously enough, the rate did not show much diminution with fatigue after prolonged testing in these cases. Instead the stridulatory motion became very irregular in character though of uniform frequency, breaks occurring every three or four strokes in which no motion at all was perceptible often for a hundredth of a minute. These breaks would have seriously vitiated the results in which they occurred if included in the rate average; consequently individuals were changed with sufficient frequency to avoid them.

The writer's estimate for the number of teeth in the stridulatory file of the worker of *Aphaenogaster fulva aquia* lies between 100 and 150, with the best value 130. The average recorded rate for the 250 tests conducted with this insect was 4.1/min. $\times$ 10^{-2}, the actual, therefore, 8.2/min. $\times$ 10^{-2}, or 13.7 gastric strokes per second. This would produce a note on the basis of the above estimation of a frequency of 1781/second. The highest recorded rate, in Test 161, was 7.4, actually 14.8/min. $\times$ 10^{-2} or 24.7/sec., producing a note of 3211/sec. The lowest recorded rate was that of Test 198, it being 2.0, actually 4.0/min. $\times$ 10^{-2} or 6.7/sec. yielding a sound of frequency 871/sec. Thus with this species also all records yield pitches so far within the humanly audible range that errors of magnitude difficult to conceive would be required to place them outside.

The estimate for the number of teeth in the file of the female of *Leptothorax longispinosus* made by the writer lies between 100 and 150, with the best value 148. A female was used in these tests. The average recorded gastric rate was 6.0/min. $\times 10^{-2}$, actually 12/min. $\times 10^{-2}$ or 20/sec., producing a sound on this estimate of frequency 2960/sec. The highest recorded rate was that of Test 122, 15/min. $\times 10^{-2}$, actually 30/min. $\times 10^{-2}$ or 50/sec., producing a note of frequency 7400/sec.—the highest recorded, but still relatively low. The lowest rate was recorded in Test 2, 2.5/min. $\times 10^{-2}$, really 5/min. $\times 10^{-2}$, or 8.3/sec., producing a tone of 1228.4 vibrations per second. Again all records indicate that the notes produced were so low in frequency as readily to induce forced vibrations in fairly massive media.

An error of unknown magnitude, but, as Sharp (1893) has shown, certainly not possibly more than 50%, was introduced in the final series of tests by the necessity of estimating the number of file-ridges in the perfect female of *Solenopsis molesta* while counting the gastric strokes in stridulation in the worker. The estimate made for the file-ridges lay between 100 and 150, with the best value at 130. The average recorded rate of gastric motion was 4.7/min. $\times 10^{-2}$, actually 9.4/min. $\times 10^{-2}$ or 15.6/sec. producing a note of 2028/sec. The highest value taken was that of Trial 157, 8.5/min. $\times 10^{-2}$, actually 17.0/min. $\times 10^{-2}$, corresponding to a note of frequency 3705/sec. The lowest value was recorded in Test 59, it being 2/min. $\times 10^{-2}$, really 4/min./100 or 6.7 per second, which would yield a pitch of 871/sec.

It seems clear that the pitch of the sounds given out by these four small Myrmicine ants in stridulating which, it is believed, may justly be taken as typical, is not only sufficiently low to readily induce vibrations in material media, but to be well within the scope of human powers of hearing—so far, indeed, that errors of very large magnitude would be necessary if the conclusion were to be drawn that they were actually supersonic in character.

While it is of course intrinsically evident that the sounds emitted by the audibly stridulating *Ponerinae* are sufficiently low in pitch to produce forced oscillations readily enough, an estimation of this pitch seemed desirable. The method used was essentially that already described. The stridulatory motion cannot be detected in living *Ponerinae*, both because of its infrequency and because the generalization of the segments involved permits no such marked articulation as obtains with Myrmicine ants. Because of this difficulty of articulation, moreover, the *Ponerinae* rarely employ the whole file in the process, scraping only a variable and indeterminate portion of it.

Tests with living insects similar to those conducted on the Myrmicines were therefore out of the question. The stridulatory motion, however, can readily be reproduced in dead specimens with appropriate results, and in such case the use of the entire file is assured. Two of the three quantities sought are unknown, however—the rate of gastric motion and the pitch of the sound. It is necessary in this case to adjust the pitch of sound produced artificially to that of the living insect, and this adjustment which in the present state of development of sound amplification devices can only be made by ear is doubtless the greatest source of error in the experiment. The pitch having been adjusted to that normally produced, as closely as can be determined by ear, the rate of motion of the scraper is easily measured and the number of file ridges estimated and the probable pitch determined as before. Inaccurate as such a method must be, it is still sufficiently exact for present purposes, since it was found impossible, in the specimens measured, to operate the file and scraper sufficiently rapidly to produce sounds remotely approaching the upper limit of hearing of the operator.

It was found more convenient in practice to substitute a keen razor for the natural scraper, a procedure which did not materially affect the quality of the sound and which permitted greater precision of measurement. The workers of two species were used, both of which normally stridulate audibly: *Paraponera clavata* and *Neoponera villosa*. When the pitch had been adjusted in these two cases, the rate of motion of the razor was found to average respectively 4.7 and 6.6 strokes per hundredth of a minute, or 7.9 and 11 strokes per second. The number of file ridges was estimated as limited by 140 and 160, with the best value at 156, for *P. clavata*, and as lying between 140 and 160, with the best value at 154, for *N. villosa*. The note given out by the former species would thus be of a frequency of 1234/sec., and for the latter 1694/sec. It is interesting to notice that these pitches do not lie outside the lower limit of those of stridulatory notes produced in the *Myrmicinae*, the much greater coarseness of the file-ridges in these Ponerines being compensated by the greater elongation of the specialized area.

In view of these results, it is the opinion of the writer that the objection which might be raised to the belief that stridulatory sounds are normally perceived by ants as vibrations of material media, either forced or directly transmitted, to wit, that these sounds are of too high a frequency to induce such vibration, is without validity. The following conclusions are offered, in view of the material presented in the foregoing paper.

Conclusions

The ability to perceive aerial vibrations, an ancient Orthopteroid characteristic, has been retained in ants, though in diminished degree corresponding to the diminution in power and perfection of the chordontal organs. The significance of such aerial vibrations, and the attention bestowed upon them, has diminished markedly. Under ordinary conditions the power to sense aerial vibrations is allowed to lapse, and the sensing of sounds produced within the nest is nearly or entirely mechanical, involving a tactile rather than an auditory—in the usual meaning of the term—sense. Furthermore, the sounds produced by the ants themselves within the nest, in particular those produced by stridulation, are mechanically perceived through vibrations set up in the surrounding solid medium, either directly transmitted from the body of the sound-producer, or induced forcedly in the medium by aerial vibrations. Stridulatory notes are of such a frequency as to make this readily possible.

Summary

The question of the existence of a power in ants to sense vibrations aerially transmitted was investigated as early as 1810 by Pierre Huber. Since the time of Huber a very large number of workers—Forel, Emery, Wheeler, Landois, Lubbock, Janet, Miss Fielde, Turner, Parker, Metcalf, Weir, Weld, Miss Wagner and others—have entered the field, and have obtained surprisingly contradictory results. Thus Huber, Forel, Miss Fielde, and Parker all concluded that this power was wanting, Weir believed it present for sounds above the humanly audible range but wanting in sonant aerial vibrations, Lubbock was uncertain, while Landois, Metcalf, Wasmann, Weld, and Turner have all recorded experiments indicating its existence, and Wheeler has summoned extraneous evidence to the same conclusion.

It is clear that sonant vibrations perceived by ants as oscillations in material media may arise either as waves directly transmitted to the subjects from the sound-producer by an unbroken chain of rigid substances, or may arise as forced vibrations in the medium with which the ants are in contact, there being only an air connection between it and the producer of sound. Nests of three types were devised for use in the present experiments, with this in mind, the first being made of glass, the second of putty, and the third of cotton. All were carefully insulated from mechanical shock. The first two would presumably admit some forced vibrations, especially the former, but the last was designed to exclude all mechanical oscillations.

Tests were made with a carefully calibrated pitchpipe, embracing the chromatic scale, C to C, A 440 pitch, on twenty-five species of ants, the Ponerine, Dolichoderine, Myrmicine, and Formicine subfamilies being represented. Tests were also made with six species in glass nests similar to those used in the regular tests, but long inhabited by the insects tested, to give some indication of the direction and magnitude of the psychological factor in affecting response under unfamiliar conditions. 2079 tests were made and considered worthy of record, of which 2.12% evoked striking reaction in the subjects, 14.05% evoked equally positive but less striking response, 19.34% showed reactions which might be interpreted positively but cannot certainly be so presented, while 64.50% were negative or only negligibly positive. No species failed to give a slight possible reaction in the cotton type of nest, while five species, two Ponerine, one Myrmicine, and two Formicine, failed to give slight positive reaction, and fifteen, four Ponerine, four Myrmicine, one Dolichoderine, and six Formicine, failed to react markedly. The distribution of these results indicates that the non-reactive cases were failures of psychic responses rather than of perception. It is concluded that the ants tested possessed the power to sense sonant aerial vibrations, and indicated that the power may be general.

The foregoing tests, though indicating the existence of an auditory power, evidence it to be normally very slightly employed. Tests involving the use of material vibrations of the same frequency would show a much higher percentage of positive reactions. The significance of aerially transmitted vibrations as messengers of danger is much less than that of those mechanically perceived. It would seem very natural that ants, considering their habitat, should habitually perceive sounds, whether originating outside of the nest or within as stridulations of their fellows, mechanically.

Such a conclusion would demand a divergence between the results obtained in the experiments with glass and putty nests, the former being much more susceptible to forced vibrations. This condition was experimentally fulfilled, 29.34% of the tests conducted in the former type eliciting response, against 22.89% in the latter. The divergence should probably be greater, since visibility was much better in the putty type of nest so that responses were more easily detected there, and the instinct to excavate in the earth-filled glass nests often excluded other stimuli. The magnitude of this factor is indicated by the tests with other colonies, in which 52.62% of the tests elicited response, while but 25.65% were reacted to by the same six species in earth-filled nests with which they were unacquainted.

The conclusion that the stridulatory notes are not perceived aerially is strengthened by the fact that there is no correlation to be found between the power to sense aerial vibrations as indicated by the tests and the development of the stridulatory organ. Thus 40.78% of the reactions obtained for all species were elicited from Formicine and Dolichoderine ants, comprising 40% of the species tested. *Stigmatomma pallipes*, a Ponerine, possesses no stridulatory organ yet responded in 80% of the tests on it, while *Ponera coarctata*, possessing a well-developed file, reacted in but 40% of the cases. The lesser perfection of the chordontal organs in ants over inferior orders suggests the same conclusion.

There is much reason to believe that stridulatory notes, if not sensed aerially, are nevertheless perceived. This is indicated by the complex social use to which the power has been shown to be put, and by the extraordinary correlation which exists between the perfection of the organ structurally and in function and in social advancement in the Ponerines. The conclusion that stridulatory notes are therefore mechanically perceived is further suggested by the absence of the organ in the Dorylines, a subfamily living much in the open air, but whose social habits would otherwise seem to make it a highly useful tool. The same conditions obtain in the tribe *Cryptocerii* of the *Myrmicinae*, composed of ants almost wholly arboreal in habit. The absence of the stridulatory organ in the Dolichoderines and Formicines is not so simply explicable, however, since no degenerative development from earth-living to arboreal types can be found. It is apparently due to the operation of a much more complex set of conditions.

One serious objection to the conclusion of normal mechanical perception of the stridulation through vibrations of media forced by aerial waves is the usual assumption which has been made that the pitch of the note emitted by inaudibly stridulating species, especially of the *Myrmicinae*, is of extremely high frequency. It would be difficult to suppose aerial vibrations above the limit of human audibility, for example, capable of forcing perceptible mechanical vibrations even in very light and rigid media. Tests made on *Myrmica scabrinodis sabuleti*, *Aphaenogaster fulva aquia*, *Leptothorax longispinosus*, and *Solenopsis molesta* indicate this assumption to be false, removing the difficulty. The highest, lowest, and average frequencies found for these four species were respectively 3215/sec., 583.4/sec., 2001/sec.; 3211/sec., 871/sec., 1781/sec.; 7400/sec., 1228.4/sec., 2690/sec.;

3705/sec., 871/sec., and 2028/sec., all well within the audible human range. Tests of similar character were made on the audibly stridulating Ponerines *Paraponera clavata* and *Neoponera villosa.* The average frequencies obtained for these species were respectively 1234/sec. and 1694/sec., well within the region of the Myrmicine species tested.

It is concluded that in the ants tested the power to perceive aerial vibrations is present, but only as an archaic relict. It finds little or no normal use in the nest under ordinary circumstances of life, nest-sounds, including stridulation, being perceived mechanically.

Literature

Adlerz, Gottfried Agathon, 1858–1918.

1896. Stridulationsorgan och ljudförnimmelser hos myror. Oefv. Vet.-Akad. Förh. 52: 769–782. 1896.

Allard, Harry Ardell, 1880–

1928. Specializations governing musical expression among insects. Sci. Monthly 27: 81–88. *illust.* Jl 1928.

Blanford, Henry Francis, 1834–1893.

1881. Sound-producing ants. Nature 25: 32. 10 N 1881.

Dichtl, Al.

1924. Einige Versuche über den Erschütterungssinn der Ameisen. Zeits. Wiss. Insektenbiol. 19: 100, 101. 1924.

Eidmann, Hermann, 1897–

1925. Das Mitteilungsvermögen der Ameisen. Naturwissenschaften 13: 126–128. 1925.

Emery, Carlo, 1848–1925.

1893. Zirpende und springende Ameisen. Biol. Centr. 13: 189, 190. 1 Ap 1893.

Fielde, Adele Marion, 1839–1916; & Parker, George Howard, 1864–

1904. The reactions of ants to material vibrations. Proc. Acad. Nat. Sci. Phila. 56: 642–650. *illust.* 2 N 1904.

Forbes, Henry Ogg, 1851–1932.

1881. Sound-producing ants. Nature 24: 101, 102. 2 Je 1881.

Forel, Auguste Henri, 1848–1931.

1888. Expériences et remarques critiques sur les sensations des insectes. Rec. Zool. Suisse 4: 1–50, 145–240, 515–523. *pl. 1.* 1888.

Fotheringham, John

1881. Sound-producing ants. Nature 25: 55. 17 N 1881.

Fulton, Bentley Ball, 1889–

1928. Sound-perception by insects. Sci. Monthly 27: 552–556. D 1928.

Graber, Veit, 1844–1892.

1882. Die chordotonale Sinnesorgane und das Gehör der Insecten. Arch. Mikr. Anat. 20: 506–640. *pl. 30–35* + *f. 1–6.* 1882.

Gounelle, Émile, 1850–1914.

1900. Sur les bruits produit par deux espèces américaines de Fourmis et de Termites. Bull. Soc. Ent. France 1900: 168, 169. 1900.

Hingston, Richard William George, 1887–

1924. The evolution of the faculty of communication in ants. Rep. Proc. Fifth Ent. Meeting (Pusa, 1923). 289-295. 1924.

Huber, Jean Pierre, 1777–1840.

1810. Recherches sur les moeurs des Fourmis indigènes. 1–138. *pl. 1, 2.* 1810.

Janet, Charles, 1849–1932.

1893a. Marques extérieures correspondants aux organes chordotonaux des Fourmis. Bull. Soc. Ent. France 1892: 247, 248. 1893.

1893b. Sur la production des sons chez les Fourmis et sur les organes qui les produisent. Ann. Soc. Ent. France 62: 159–168. 1893.

1894a. Sur l'appareil de stridulation de Myrmica rubra L. Ann. Soc. Ent. France 63: 109–117. *f. 1, 2.* Ap 1894.

1894b. Sur les nerfs de l'antenne et les organes chordotonaux chez les Fourmis. Compt. Rend. Acad. Sci. Paris 118: 814–817. *f. 1, 2.* Ap 1894.

1894c. Sur l'anatomie du pétiole de Myrmica rubra L. Mém. Soc. Zool. France 7: 185–202. *f. 1–6.* 1894.

Krausse, Anton Hermann, 1878–

1910. Ueber Stridulationstöne bei Ameisen. Zool. Anz. 35: 523–526. 15 Mr 1910.

Landois, Hermann, 1835–1905.

1874a. Thierstimmen. 1–229. 1874.

1874b. Ueber die Sprache der Ameisen. Verh. Nat. Ver. Preuss. Rheinl. 31: Corresp. 69, 70. 1874.

Lewis, David Morgan, 1851–

1882. Sound-producing ants. Nature 25: 266. 19 Ja 1882.

Lewis, Richard Thomas, 1839–1916.

1896. Note on a stridulating organ in a South African ant, Streblognathus aethiopicus. Jour. Quekett Micr. Club II. 6: 271–274. *pl. 12.* N :

Lubbock, John, Lord Avebury, 1834–1913.

1882. Ants, bees, and wasps. 1–448. *pl. 1–5.* 1882.

Metcalf, Maynard Mayo, 1868–

1900. Hearing in ants. Science II. 11: 194. 2 F 1900.

Peal, Samuel Edward, 1834–1897.

1881. Sound-producing ants. Nature 24: 484. 22 S 1881.

Rádl, Emanuel, 1873–

1905. Ueber das Gehör der Insekten. Biol. Centr. 25: 1–5. 1 Ja 1905.

Sharp, David, 1840–1922.

1893. On stridulation in ants. Trans. Ent. Soc. London 1893: 199–213. *pl. 9.* Je 1893.

Siebold, Carl Theodor Ernst von, 1804–1885.

1844. Ueber das Stimm- und Gehörorgan der Orthopteren. Arch. Naturg. 10^1: 52–81. 1844.

Swinton, Archibald Henry

1878. Note on the stridulation of Myrmica ruginodis and other Hymenoptera. Ent. Monthly Mag. 14: 187, 188. Ja 1878.

Turner, Charles Henry, 1867–1923.

1907. The homing of ants: an experimental study of ant behavior. Jour. Comp. Neur. Psychol. 17: 367–434. *pl. 2–4 + f. 1.* S 1907.

Wacker, Franz

1925. Beiträge zur Kenntnis der antennalen Sinnesorgane der Hymenopteren. Zeits. Morph. Oekol. Tiere 4: 739–812. *pl. 16, 17 + f. 1–44.* [N] 1925.

Wasmann, Erich, 1859–1931.

1893. Lautäusserungen der Ameisen. Biol. Centr. 13: 39, 40. 1 F 1893.

Weir, James, 1856–1906.

1898. The ears of worms, crustaceans, and ants. Sci. Am. 78: 282. 30 Ap 1898

Weld, LeRoy Dougherty, 1880–

1899. The sense of hearing in ants. Science II. 10: 766–768. 24 N 1899.

Wheeler, William Morton, 1865–1937.

1903. Ethological observations on an American ant (Leptothorax emersoni Wheeler). Jour. Psychol. Neurol. 2: 31–47. Ap 1903; 64–78. Jl 1903.

Wroughten, Robert Charles, 1849–

1892. Our ants. Part I. Jour. Bombay Nat. Hist. Soc. 7: 13–60. *pl. A, B.* 1 Je 1892;—Part II. Jour. Bombay Nat. Hist. Soc. 7: 175–203. *pl. C, D.* 1 O 1892.

Explanation of Plates I–V

(All figures × 150)

Plate I

Neoponera villosa ☿ Mid-dorsal surface of protected portion of third abdominal segment, showing specialization of stridulatory file

Plate II

Figure 1 *Ponera coarctata pennsylvanica* ☿ Dorsal view of second and third abdominal segments bent to expose the stridulatory file

Figure 2 *Lobopelta elongata* ☿ Dorsal view of file

Figure 3 *Paraponera clavata* ☿ Dorsal view of mid-portion of file

Plate III

Figure 1 *Pachycondyla harpax* ☿ Dorsal view of area homologous with Plate II figure 3, showing absence of specialization as a file

Figure 2 *Proceratium croceum* ♀ Same as preceding

Plate IV

Figure 1 *Eciton hamatum* ♀ Dorsal view of protected portion of third abdominal segment, showing absence of specialization as a file

Figure 2 *Eciton hamatum*, ☿ Lateral view of first abdominal (first petiolar) segment, showing lack of specialization on this region

Plate V

Figure 1 *Cryptocerus* sp ☿ Dorsal view of protected surface of third abdominal segment, showing absence of specialization

Figure 2 *Cephalotes* sp ☿ Same as preceding

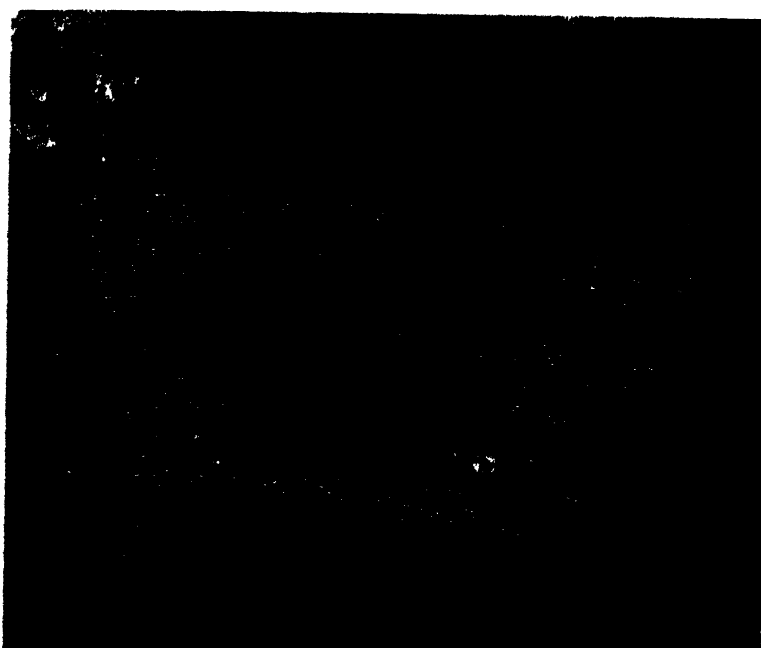
Figure 3 *Myrmica scabrinodis sabuleti* ☿ Dorsal surface of protected area of first gastric segment, showing left half of stridulating band

Figure 4 *Aphaenogaster fulva aquia* ☿ Same as preceding, showing median portion of stridulating band

Figure 5 *Leptothorax longispinosus* ♀ Same as preceding

Figure 6 *Solenopsis molesta* ♀ Same as preceding, showing right half of stridulatory band

HASKINS AND ENZMANN FORMICIDAE

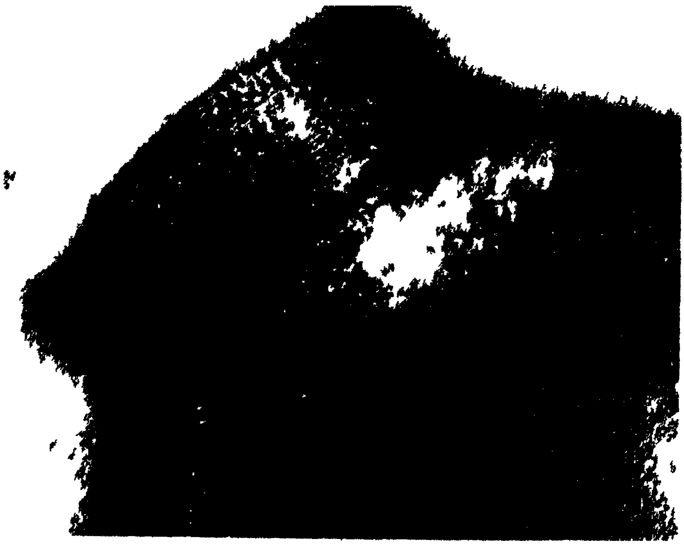


3

HASKINS AND ENZMANN FORMICIDAE

2

HASKINS AND ENZMANN FORMICIDAE



2

HASKINS AND ENZMANN FORMICIDAE

1

2

3

4

5

6

HASKINS AND ENZMANN: FORMICIDAE

PART II

TYPES OF COLONY-INITIATION IN THE PONERINAE AND DEGENERATION OF WING-MUSCULATURE IN THE QUEEN

Historical Review

The method of colony-formation among higher ants is so well known, and has so often been observed, as scarcely to bear repetition in description. It was first observed by Pierre Huber (1810), by Mayr (1864), and by Lincecum (1867). It has since been described in detail by McCook (1879) and Lubbock (1882), and a host of later workers, and its sociologic implications have been considered by Wheeler (1910)

The possible phylogenetic significance of colony-foundation by isolated females in the *Formicidae*, with its implication that the mature ant colony represents merely an enormously enlarged family in which the life of the female has been greatly prolonged relative to the longevity of the progeny, makes it especially desirable that information should be available concerning the phenomenon in the socially most primitive subfamily, the *Ponerinae.* The *Ponerinae* comprise a group in which the foundation of colonies is, on the whole, difficult to observe experimentally. Wheeler has observed the formation of colonies by isolated females of *Odontomachus haematodes*, and this would seem indeed to be the normal method of the genus. Observations of other species, however, have been largely lacking. The question is the more interesting because of the possible implications afforded by certain parallel physiological phenomena which normally accompany the process in higher ants. It is well known, as Janet (1906, 1907a, 1907b) has shown for *Lasius niger*, that, immediately following dealation in the fertilized female, a degeneration of wing-musculature begins, apparently accomplished by the action of amoebocytes, whereby the striated muscle structure is replaced by fat-granules. A portion of these passes to the ovaries to assist in bringing the first eggs to maturity, while the remainder is transferred to the region of the salivary glands and serves to feed the developing larvae. Because of this situation, and the extreme discrepancy in bodily size which exists between the normal fertile female of the higher ants and the first brood of miniature prematurely pupated adults, it is possible for the young queen to bring to maturity the first brood of workers without partaking of food. The young female is thus enabled to remain walled in a cell without seeking food during the incubation period of the young.

So far as known to the authors, no previous investigation has been made of the condition of the wing-musculature in alate females of Ponerine genera. However, even were degeneration of wing-muscles to take place in the lower as in the higher ants, the ability of young females to establish independent colonies without food should be seriously questioned, because of the similarity in stature of queens and workers in the group as a whole, and the inability of first-brood young to pupate prematurely. Further doubt is cast by the fact that many Ponerine larvae are exclusively entomophagous, the method of feeding habitually employed by the nurses consisting in the distribution of fragments of captured insects or other Arthropods among the larvae. It is doubtful if such larvae would accept ingluvial food if it were offered.

These conditions have led Wheeler to postulate a method of colony-formation among primitive Ponerines by means of "partial provisioning." The female is supposed to isolate herself with her first packet of eggs in a cell, as with the higher ants, but to construct a passage from the cell to the outer environment, leaving frequently to forage. If the species is epigaeic, the female undoubtedly forages on the open ground, if hypogaeic, as in so many of the more timid Ponerine races, the foraging is presumably subterranean. Wheeler (1932) was able experimentally to confirm his assumption among the primitive Ponerines of the Australian genus *Myrmecia*, which are known to have a true nuptial flight, in very striking fashion.

Methods

It is the purpose of this paper to assemble data obtained during eleven years of work which, it is hoped, may help to shed a little additional light upon the problem. In keeping with their enormous antiquity, the *Ponerinae* present a series of enormous diversity in all their habits of life, ranging from the highly epigaeic, semi-arboreal *Ectatomii* and *Odontomachii*, so active in habit and so highly specialized in structure as to resemble the higher more nearly than the primitive forms, to the extremely timid, completely hypogaeic *Amblyoponii*. Nuptial flights are well known in the former types, and it is not difficult, especially in the American tropics, to find young colonies of ants of these tribes, founded in each case by a single queen, in all stages of development, although it does not seem probable that the procedure has faithfully paralleled that of the higher ants. In contrast, little or nothing has been published concerning the nuptial flight of ants of the hypogaeic *Amblyoponii* or *Ponerii*, and, although

the present writers believe that they have elucidated this satisfactorily, isolated females of the two species studied have never been found during many years of fairly intensive search.

In an attempt to obtain a very little evidence for this gap in our knowledge, several species of ants were selected for study with reference to the methods of colony-formation employed by their fertile females. It is hoped that they represent a fair "sampling" of the Ponerine group as a whole.

Notes are presented on the procedure observed in colony-formation alone (since nuptial flights have already been reported for all but the last) in *Odontomachus haematodes* and its variety *insularis*, *Paraponera clavata*, *Pachycondyla harpax*, *Euponera stigma* and *Proceratium croceum*. The species *Stigmatomma pallipes* and *Ponera coarctata pennsylvanica* were selected as typical of those timid, hypogaeic forms of Ponerines in which nothing is known concerning either the nuptial flight or the method of colony-foundation. For these, a summary is presented of a fairly intensive study of the nuptial flight, made over a period of twelve years. But little information can be given of the course of colony-formation with these species, however, in spite of prolonged observation of fertile females both in the wild state and in the artificial nest. It may nevertheless be possible to draw certain general conclusions.

The results of a study of the fate of the wing-musculature in certain of the more primitive Ponerine types are then presented.

Formation of New Colonies

I. *Odontomachus haematodes*, and var. *insularis*.

This ant, in its type form or one of its numerous subspecies, is common to the tropics around the world. Isolated females are by no means difficult to discover in situations occupied by the type. They have been reported by Wheeler, together with the allied species *O. clarus*, and have been observed by the present authors in Bermuda, the Philippine Islands, Java, and on Barro Colorado Island. Fertile females are difficult to discover in adult colonies, and more than one is rarely found in a single nest, indicating that isolation of young females is probably the usual procedure.

Nine queens of *Odontomachus haematodes insularis* were taken in Bermuda in 1929, isolated in individual cells, several of which contained egg-packets. They were set aside for observation in artificial nests. All immediately formed well-built cavities analagous to those of the higher ants, but open at one side. Eggs were shortly deposited

by five of these females, formed into packets as with the higher ants, and given continuous attention. All of the queens continued to forage actively during this period, returning to the brood-chamber with the provender as secured, and devouring it there. The young larvae were individually secured to the roofs of the brood-chambers as soon as hatched, in the fashion typical of the genus, and were fed, so far as observed, entirely on fragments of insect or mammalian tissue obtained outside the formicary, dissected, and placed within reach of the young. As these matured, they were allowed to lie singly on the floor of the chamber ventral surface upward, and similar provender was laid on the trough-like depression of the abdomen. Cocoons were spun by the larvae within three months, and were abnormally small. Such cocoons were found with wild isolated females of the subspecies in Bermuda, and have been taken in numerous incipient colonies of the type on Barro Colorado Island. Both those formed in artificially housed colonies and those taken in a natural environment enclosed perfect, but fairly diminutive, workers. No evidence has been secured that first-brood workers are fed on salivary fat-body, although evidence will be presented to indicate that such a food supply is apparently present. Indications are definitely contrary to this. Partial provisioning would seem to be the rule.

II. *Paraponera clavata.*

The colonies of this widely-distributed, well-known, and much-feared large Ponerine of the American tropics normally contain many queens. The condition has been reported by a number of workers and has been noticed by one of us in all of the colonies (some ten) personally excavated and examined on Barro Colorado Island over a period of years. This suggests that young and freshly fertilized queens may on occasion return to the parent colony. The queens emerge, as though for a true nuptial flight, irregularly throughout the year, and the males fly strongly and readily, coming often to lights. Young, freshly dealate queens have been taken in the open on Barro Colorado. They are difficult to maintain for any length of time in confinement under artificial conditions. One, however, was satisfactorily established. An open chamber was built, from which the insect foraged, and to which it returned to devour the prey as captured. Evidence indicated partial provisioning as the normal procedure.

III. *Pachycondyla harpax.*

Isolated females of this species, either with or without larvae and cocoons, have been found in a number of instances on Barro Colorado

Island by the authors, and in British Guiana by Dr. N. A. Weber, to whom we are indebted for some of the material used. Under artificial conditions an open cell was formed, and the identical method of partial provisioning adopted, the queen feeding actively throughout.

IV. *Euponera (Trachymesopus) stigma.*

The evidence of the method of colony-formation obtaining with this active but apparently hypogaeic Trinidad Ponerine is based upon the observation of a single individual, but is sufficiently clear-cut to be worthy of mention. The ant concerned was taken with a group of isolated females of its species from a rotten log in the Nariva Swamp, Trinidad. Under artificial conditions a large, open cell was constructed. Within this was built a much smaller, nearly closed chamber. Eggs were deposited, formed into a packet, and placed within this cell, which was too small to be fully occupied by the adult. The female visited the cell many times a day, thrusting the head and the fore portion of the thorax into it after the fashion of the wasps of the genus *Polistes.* The queen actively foraged during the period of incubation of the eggs. Insect material, as obtained, was brought into the larger chamber for consumption. As soon as the ovae closed, fragments of insects were distributed among the larvae in the small cell. When the larvae were half grown, the auxiliary chamber was demolished and the larvae moved to the main brood-chamber where they continued development, still abundantly supplied with insect food. Partial provisioning, again, was the method used in colony-foundation, although a section of the thorax of the queen, as will later be indicated, showed complete degeneration of the musculature, so that fat-body was in all probability available. At no time, however, were the larvae observed to be fed by regurgitation.

V. *Proceratium croceum.*

Three young fertile females of *Proceratium croceum,* obtained through the kindness of Dr. M. R. Smith, were placed together in an earth-filled Lubbock nest, and observed over a period of nine months. All three immediately constructed cells, one isolating itself, the other two constructing a common chamber. Eggs were shortly laid, formed into a packet, and the larvae hatched and reared partly to maturity, being given consistent attention by the adults during this time. Partial provisioning was the rule throughout, and the larvae, despite their relative inactivity, were fed only on fragments of insect material distributed among them, so far as could be observed. Certain it is that, when such insect food was withheld, the larvae showed greatly delayed or completely arrested growth and development.

Little is known of the nuptial flight of this species. Considerable numbers of young queens are produced in the colonies, becoming fully pigmented before leaving the nest. Again thanks to the courtesy of Dr. Smith, the writers were privileged to observe a group of six young infertile females, taken from a single colony, over a considerable period of time. All dealated themselves without leaving the nest, after the fashion commonly practiced by a number of other Ponerines under artificial conditions. Observations of the authors on *Stigmatomma* and *Ponera* have indicated that this is not correlated with the absence of a true nuptial flight. Placed in a single group in a Lubbock nest containing decayed wood closely simulating their natural environment, these females of *Proceratium* isolated themselves, and some laid eggs and hatched and reared larvae, precisely as did their fertile sisters.

It appears that the fertile females of *Proceratium croceum* are capable of independently forming new communities, with partial provisioning, in the fashion of the other species discussed. Their normally hypogaeic habits, however, together with the multiplicity of females often found in a single colony, suggest that in addition young queens may after fertilization (taking place perhaps on the ground) return to the parent colony, which then reproduces by fission. In such case, of course, neither the habit of partial provisioning nor the physiological condition of degenerate wing-musculature would be of assistance. That such a habit and condition may, nevertheless, coexist with that of forming independent communities—or may even be dominant to it—in a number of Ponerines, has been strongly indicated by rather more extended observations which we have been able to make on the completely hypogaeic *Stigmatomma pallipes* and *Ponera coarctata pennsylvanica*, which are summarized below.

VI. *Stigmatomma pallipes* and *Ponera coarctata pennsylvanica*.

The first species, which is widely but locally distributed over the American continent, belongs to the tribe *Amblyoponii*, which includes several archaic and interesting genera such as *Amblyopone*, *Mystrium*, and *Prionopelta*. The second belongs to the highly diversified tribe *Ponerii*. Both are ancient timid forms, dwelling in small colonies, the workers with almost or completely vestigial eyes and nearly or entirely hypogaeic in habit. Although very nearly as primitive as *Myrmecia* in social organization and in most of their habits, these ants are clearly less representative of the ancestral Formicine type. Their extreme timidity suggests long contact with more vigorous, progres-

sive, and prolific species, and has led, at least in the case of *Stigmatomma,* to an apparent specialization in the diet. It would not be surprising to discover a similar specialization in the method of colony-formation. Whether the method of colony-formation by fission represents such a specialization may be open to question. That it is normal with this species seems to be definitely established from a continuous series of investigations, begun in 1924, and extending with relatively little interruption over a twelve-year period.

The earliest observations of the authors indicative of a true nuptial flight in *Stigmatomma pallipes* were made with artificial, earth-containing Lubbock nests, in which small colonies, which later produced winged forms, had been relatively well established. Males emerged readily and in numbers, but only two females left the colonies. Both were callow, one having retained the wings, the other having cast them within the formicary. This habit has been very commonly observed in this and a number of other species of Ponerines under artificial conditions, but has never been seen in wild colonies. Similar observations were made the following year, when numbers of males emerged readily from artificial formicaries. The young queens, however, were excessively timid, and, although repeatedly clustering about the nest-entrances, were very hesitant in exposing themselves. Finally, however, by inclining the nest-cases and arranging a gradient both of light and moisture from the open entrance to the interior, twelve females were induced to emerge. All were unaccompanied by workers or males. Eight were winged, the remaining four having cast the wings before leaving. All were still in the red, callow condition. Most of these individuals remained relatively quiet after emergence, but one ran actively toward the light and took flight. At the same time a number of wild males of the same species, many still living, and a single callow winged female were recovered from a pool of water in a woodland known to contain the species, indicating that under natural conditions the queens as well as the males may sometimes fly actively. The following year it was possible to observe the emergence of a young queen from a wild colony under entirely natural circumstances. No flight took place, however, the female soon returning underground. The next year three young queens, winged and callow, were taken living from water-traps so placed that they could not well have been entered except from the air. One of these insects, when released, repeatedly flew strongly, although struck to the ground several times to permit of further observation. No males were in evidence. In 1928 young queens were again induced to leave artificial

nests, in every case in the callow condition. Young callow queens were seen to fly again in 1929, 1930, and 1932, and confirmatory observations have been made in subsequent years, leaving little doubt that this at times, at least, is the normal procedure.

At no time, however, has mating been seen to take place in flight. Actual fertilization of the queens apparently always takes place on the ground or on slight elevations, the active, low-flying males seeking out the resting females, in marked contrast to the mating procedure of higher ants. This was indicated under artificial conditions when young females placed in large boxes containing males which had emerged from artificial nests were quickly found and fertilized, the males flying almost directly to them. It was rather clearly shown under natural conditions also. Twelve callow queens, both winged and dealate, were exposed on successive days in an open field. Each, after a few moments, exhibited a marked tropic shift from negative to positive, mounted a convenient twig, and remained quiet. Within a few moments numbers of males of the species were attracted, flying close to the ground, and the queens were quickly located. All the females, after fertilization, returned to the ground and entered it at the most convenient point.

The identical mating procedure has been noticed repeatedly since 1925 with *Ponera coarctata pennsylvanica*. Queens have never been seen to be fertilized except when resting. It is clear, however, that the females do have a dispersion flight. They have been taken repeatedly from water-traps, and on one occasion literally hundreds were seen in a single day flying or recently descended on the campus of Cornell University. Young queens of *Ponera* appear always to become fully pigmented before flight.

It seems clear that we are dealing with a modification of the mating flight of *Myrmecia* which corresponds quite closely with the habitus of these types. The power and habit of flight are retained by both sexes, but the latter is apparently much reduced in the females, some of which never seem to move far from the entrances of their own colonies. The promptness with which females reenter the soil when fertilized suggests that many may return at once to their own formicaries. The surprisingly large number of queens found in many relatively small colonies of *Stigmatomma* and *Ponera*, especially at the close of the season of flight, aids this impression. It has been further confirmed by the finding, season after season, of dealate callow queens of *Stigmatomma* in the superficial chambers of wild colonies, in company with winged individuals waiting to emerge.

The habit of independent colony-formation is certainly not entirely lost among the hypogaeic forms, however. From some fifty young alate queens of *Stigmatomma* which have been isolated, three voluntarily formed cells. All were left permanently open at one side, and the adults left them freely to forage. In one case many eggs were laid, formed into a packet, and cared for until they were hatched. Larvae were reared nearly to maturity in the fashion practiced by the ants already discussed.

The observations recorded seem to indicate fairly clearly that the method of colony-formation by isolated females, following the method of partial provisioning described by Wheeler for *Myrmecia*, represents the ancestral type of inception of the Formicine colony and has been rather widely retained among the Ponerines in general. However, it seems probable to the writers that, at least among such timid tribes of the Ponerines as the *Amblyoponii* and certain *Ponerii*, the primitive nuptial flight of *Myrmecia* has been retained but partially modified so that mating no longer takes place in flight, while upon the ancient, imperfectly claustral method of colony-formation has been partially superposed one of the two dependent methods of initiating new communities—swarming or temporary parasitism—characteristic of the higher ants.

Degeneration of Wing-musculature

The question then arises as to how far physiological specialization, in the degeneration of wing-musculature, has progressed in the lower ants. Clearly it would be quite unnecessary for survival in forms which habitually hunt during colony-foundation, although admittedly advantageous in enabling the organism to tide over periods of famine. It would be quite useless, apparently, in cases where young females habitually return to their parent colonies. It seems clear that the specialization must have occurred at some time during the evolution of the *Formicidae* or of a wingless ancestral stirp, since it could hardly have pertained to permanently winged forms. It is therefore of considerable interest to discover whether the evolution took place, phylogenetically, before or after the discarding of the habit of partial provisioning.

Sections have been made of the thoraces of fertile and infertile females of several Ponerine species to determine this point. They are shown in the accompanying figures (PLATE VI). The Formicine species *Lasius niger* and its subspecies *americanus* were taken as base-lines because of the extensive work of Janet with the type species, which could be duplicated before further work was undertaken.

In Figures 1 and 2 are shown sections of the thoracic wing-musculature, made in paraffin, of infertile females respectively of *Lasius niger* and *L. americanus*. It will be seen that the muscles are in excellent condition in both. This is far from being true in the old dealate female, shown in Figure 3, representing the condition in an established queen of *L. americanus*. Exactly similar situations have been found with old dealate females of the Formicine ant *Camponotus herculeanus pennsylvanicus*. The figure is very characteristic of the usual state of the thoracic musculature among old fertile females of the higher ants, the tracts being almost completely atrophied, and the thoracic cavity either containing fat-granules or entirely empty.

A comparison with infertile females of Ponerine ants is provided in Figures 4 and 5, representing thoracic sections of winged queens respectively of *Ectatomma tuberculatum* (*Ectatommii*) and *Stigmatomma pallipes* (*Amblyponii*). The muscles were found in beautiful condition, showing excellent striation, with no indication whatever of atrophy. This was to be expected, as it represents the ancient Vespine condition. It is of extreme interest, however, to notice that degeneration actually does occur during the life of the Ponerine queen, exactly as in the higher ants, and irrespective of its relative uselessness in colony-formation. In Figure 6 is shown a section of the thorax of a fertile female of *Euponera stigma* which founded its colony under observation in the artificial nest, as already mentioned, and thereafter perished. This individual partook of food throughout the time of growth of the first brood, and the first brood was nourished from this provender. At no time were the larvae observed to be fed by regurgitation. Much of the food given to the queen consisted of the larvae of higher ants, providing an ample fat-body for both adults and young. Nevertheless, it was found that muscular degeneration had taken place extensively, leaving large empty cavities where even the fat-body was exhausted. No higher type of female, deprived of nourishment over a period of nine months, could show more complete atrophy.

Essentially the same situation has been found in an old female of *Odontomachus haematodes*, which had been observed to found a colony by partial provisioning. Although fed throughout the process from extraneous fat-rich sources, the muscles were so much degenerate as to lead to the complete collapse of the thorax on sectioning.

The intermediate and final stages of the condition are shown in Figures 7 and 8, representing sections of the thoraces of callow wingless and adult wingless females of *Stigmatomma*, taken from populous colonies containing many queens. They may be compared with the thorax of the winged callow represented in Figure 5. The

ant represented in Figure 7 had been but a short time divested of wings when prepared, as indicated by the body coloration, yet the beginning of tissue absorption was noticeable. This condition may first be detected as a rounding of the normally sharp edges and corners of the muscle-blocks, before actual breakdown becomes evident. The degeneration is very marked in the second figure (Figure 8), which represents an individual at least one year old which had apparently become attached to an established colony.

It would seem, then, that the physiological condition of the breakdown of muscular tissue in dealated females is a very ancient one phylogenetically. It is found widespread and of astonishingly uniform character among diverse tribes of the Ponerines, and parallels quite closely the similar state in higher ants. Despite the fact that it plays an extremely useful role among the higher ants in permitting young females to maintain themselves and to bring their first young to maturity without the necessity of foraging, it clearly antedates that habit, and is well developed in forms which habitually employ methods of partial provisioning, as well as in those in which the function of colony-formation would appear to be at least partially lost. It would be of great interest in this connection to undertake investigation of the similar condition in the *Scoliidae*, the *Mutillidae*, and other groups, closely allied to ants. Such work is planned for the future. So highly specialized a physiologic peculiarity, restricted so closely to the Formicidae and developed so independently of other habits, might well constitute a useful criterion in the solution of a question which has long perplexed myrmecologists—the stock to which should be attributed the origin of a group which with little doubt has attained to the highest expression of individual plasticity and cooperative social organization in the invertebrate world.

Conclusions

It is concluded that the method of colony-formation by a single female, constructing an individual but open cell and partially provisioning the brood during the course of development, is the ancestral one among the *Formicidae*. It is widespread among the Ponerines, having been observed by Wheeler among the ants of the genus *Myrmecia*, and by the present writers in *Odontomachus*, *Paraponera*, *Pachycondyla*, *Proceratium*, and *Euponera* (*Trachymesopus*). This condition has apparently led, on the one hand, to the completely independent mode of colony-formation usual among the higher ants, in which the queen is walled into a closed cell during the entire period of development of the brood and partakes of no nourishment during this time,

the fat-body derived from converted wing-musculature sustaining both adult and young. On the other hand, there seems to have evolved from this stage a method of colony-formation widespread among the *Ponerinae,* and known for higher ants, in which fertilized young females return to their own or other colonies, remaining there for a time as surplus reproductive capacity. Eventually the colony multiplies by fission. Some evidence of this condition, such as the usual presence of numerous supernumerary females, can be found among many Ponerines. It would appear to be the usual rule in such timid hypogaeic forms as *Stigmatomma pallipes.*

It is found that the degeneration of wing-musculature in the freshly dealated female occurs precisely as in the higher ants, at least for the species *Odontomachus haematodes, Euponera stigma,* and *Stigmatomma pallipes.* The condition is thus well developed among ants in which it can be of little social benefit. It is concluded that the physiological condition must precede phylogenetically the social one, which has "adapted" the former to a useful end, and it is suggested that a thorough investigation of the fate of the wing-musculature in the fertile females of the several groups from which ants are variously believed to have been derived might shed light of considerable interest on the phylogeny of the whole question.

Summary

The method of colony-formation practiced among the subfamily *Ponerinae* of the *Formicidae* is very imperfectly known. A more complete picture of it might be of considerable phylogenetic significance because of the extremely primitive nature of this group. The phenomenon of colony-foundation among higher ants is normally accompanied by physiologic changes in the female which are highly characteristic, the most striking being the change of the wing-musculature of the thorax to fat-body. This fat reserve is passed to the ovaries and the salivary glands and permits the young queen, after descent from the marriage flight, to wall itself into a closed cell and rear a brood of extremely tiny workers without leaving the cell to partake of nourishment. Little work has been done on the condition of wing-musculature in dealate fertile Ponerine females. It has been the attempt of the present writers to gain and correlate information in these two fields for several Ponerine ants.

The results are presented of a series of observations on the method of colony-formation in several divergent Ponerine tribes—the *Ponerii, Proceratii, Amblyoponii,* and *Odontomachii.* Strong evidence has been obtained that colonies are habitually founded by isolated fertile

females which, however, forage actively during the maturation period of their young for the species *Euponera stigma, Odontomachus haematodes, Paraponera clavata, Pachycondyla harpax,* and *Proceratium croceum.* This corresponds very closely to the condition observed by Wheeler in the primitive Australian genus *Myrmecia* and called by him "partial provisioning."

The whole process of colony-formation, including the character of the nuptial flight, is very difficult to observe in the species *Stigmatomma pallipes* and *Ponera coarctata pennsylvanica,* and is very imperfectly known. The writers have found that the young females of these species emerge from the parent colony, but that the nuptial flight is abortive, fertilization taking place on the ground and the queens immediately reentering their own or other formicaries, so that the formation of new colonies by isolated individuals rarely occurs. Evidence has been found, however, that the young females even of these species occasionally fly, and may attempt to form isolated communities, partially provisioning the brood. It may be concluded that the method of partial provisioning by isolated fertile females represents the primitive habit of the ancient, generalized *Formicidae* from which, on the one hand, has developed the highly specialized method of the higher ants and on the other, the method of colony-fission with multiple queens (somewhat analagous to the "swarming" of bees) peculiar to certain hypogaeic tribes of Ponerines and various more or less aberrant higher ants.

It then becomes of great interest to learn whether the physiological condition of degeneration of wing-tissues has accompanied the development of the habit of colony-formation in which it is so useful. Investigations have been made of the condition of the wing-musculature in the thoraces of alate and wingless females of members of the Ponerine tribes *Odontomachii, Ectatomii, Ponerii,* and *Amblyoponii,* the species involved being *Euponera stigma, Tetraponera laevigata, Ectatomma tuberculatum, Odontomachus haematodes* and *Stigmatomma pallipes.* Results are presented in the accompanying plates for the genera *Ectatomma, Euponera,* and *Stigmatomma.* It was found that throughout this group, which may be considered a fairly representative sampling of the *Ponerinae,* the picture of wing-muscle degeneration was uniformly that presented by the higher ants. It will be recalled that the habit observations given earlier indicated that the habits both of partial provisioning and of fission in the formation of new communities are represented for the species considered. Under these circumstances, the condition of wing-muscle degeneration seems a

matter of considerable interest, since the fat-body provided by the process can be of no vital use in the social economy of the insects. It would seem to indicate that a rather fundamental social habit has "adapted" to its use a physiological condition which was apparently already present—has, in other words, been built around this condition.

It is suggested that the degeneration of wing-musculature in fertile females upon dealation, because of its conspicuous and sharply specialized character among ants, might lend itself as a useful tool in studies of the phylogeny of the *Formicidae* as a whole. It would be of extreme interest to follow the condition of the thoracic muscles throughout the lives of fertile females in those groups which have been variously considered the ancestral stirp of the *Formicidae* as a whole and the immediate progenitors of the *Ponerinae*. Such work is planned for the future.

Literature

Huber, Jean Pierre, 1777–1840.

1810. Recherches sur les moeurs des Fourmis indigènes. 1–138. *pl. 1, 2*. 1810.

Janet, Charles, 1849–1932.

1906. Remplacement des muscles vibrateurs du vol par des colonnes d'adipocytes, chez les Fourmis, après le vol nuptial. Compt. Rend. Acad. Sci. Paris 142: 1095–1097. My 1906.

1907a. Histolyse, sans phagocytose, des muscles vibrateurs du vol, chez les reines des Fourmis. Compt. Rend. Acad. Sci. Paris 144: 393–396. F 1907.

1907b. Histogenèse du tissu adipeux ermplaçant les muscles vibrateurs histolysés après le vol nuptial, chez les reines des Fourmis. Compt. Rend. Acad. Sci. Paris 144: 1070–1073. My 1907.

Lincecum, Gideon, 1793–1874.

1867. On the agricultural ant of Texas (Myrmica molefaciens). Proc. Acad. Nat. Sci. Phila. 1866: 323–331. [F] 1867.

Lubbock, John, Lord Avebury, 1934–1913.

1882. Ants, bees, and wasps. 1–448. *pl. 1–5*. 1882.

McCook, Henry Christopher, 1837–1911.

1879. The natural history of the agricultural ant of Texas. 1–310. 1879.

Mayr, Gustav L., 1830–1908.

1864. Das Leben und Wirken der einheimischen Ameisen. Oesterr. Revue 2^3: 201–209. 1864.

Wheeler, William Morton, 1865–1937.

1910. Ants: their structure, development, and behavior. 1–663. 1910.

1932. How the primitive ants of Australia start their colonies. Science II. 76: 532, 533. 9 D 1932.

Explanation of Plate VI

FIGURE 1. *Lasius niger.* Section of thorax of infertile winged female, showing perfect musculature.

FIGURE 2. *Lasius niger americanus.* Similar section of infertile winged female, showing identical condition.

FIGURE 3. *Lasius niger americanus.* Similar section of dealated female, long after removal of wings. Thoracic wing-musculature almost completely wanting, having been converted to fat-body.

FIGURE 4. *Ectatomma tuberculatum.* Similar section of infertile winged female, the musculature in perfect condition.

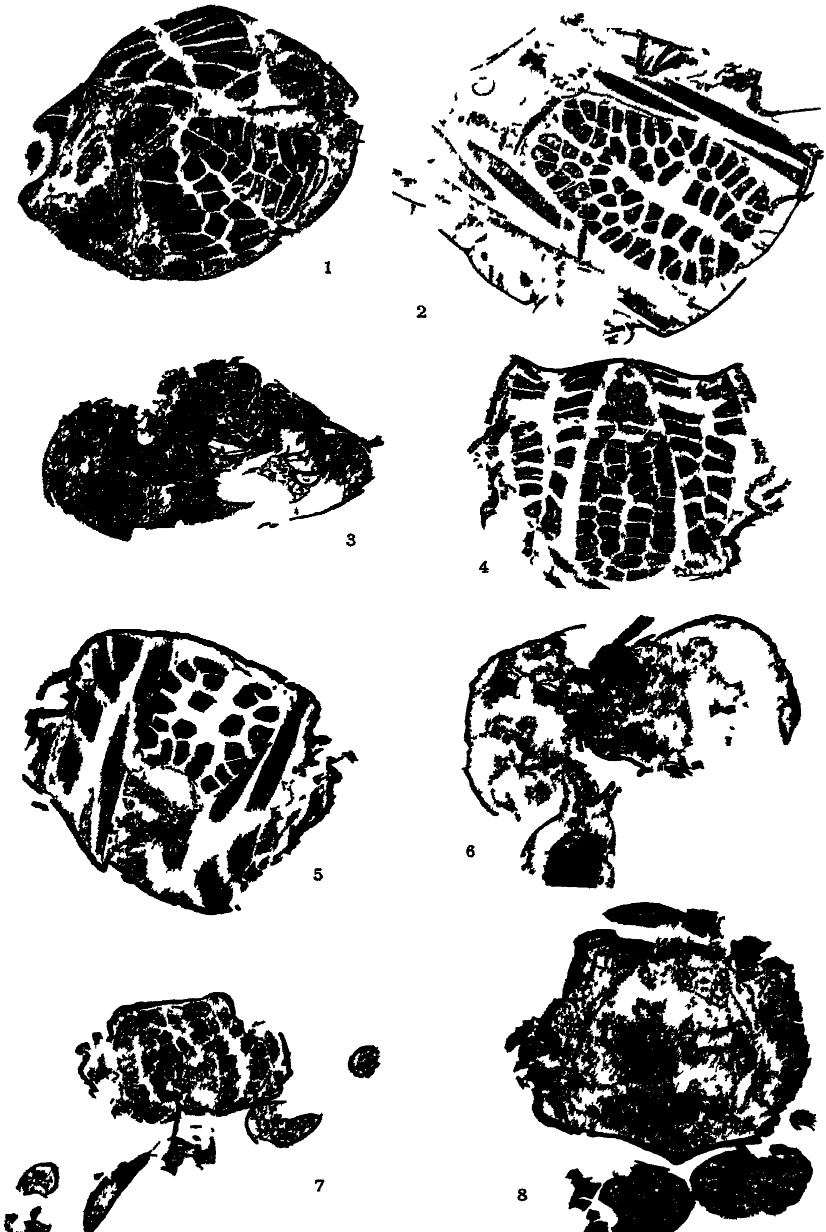
FIGURE 5. *Stigmatomma pallipes.* Similar section of infertile winged callow female, the musculature in perfect condition with visible cross-striation.

FIGURE 6. *Euponera stigma.* Similar section of fertile wingless female after founding colony. Muscles completely degenerate and thorax collapsed.

FIGURE 7. *Stigmatomma pallipes.* Similar section of fertile wingless callow female, a few days after dealation. Inception of degeneration visible as rounding of muscle-blocks.

FIGURE 8. *Stigmatomma pallipes.* Similar section of fertile wingless female, one year or more after dealation. Wing-musculature completely atrophied, with replacement by fat-body and formation of cavities.

GENERIC INDEX



HASKINS AND ENZMANN: FORMICIDAE

Annals of the New York Academy of Sciences
Volume XXXVII, pages 163–257
May, 1938

THE BROAD-SKULLED PSEUDOCREODI*

By Robert Howland Denison

CONTENTS

* Awarded an A. Cressy Morrison Prize in Natural Science in 1937 by the New York Academy of Sciences. Publication made possible through a grant from the income of the Centennial Fund.

INTRODUCTION

The present paper deals with those Upper Paleocene and Eocene carnivores grouped by Matthew (1909, p. 409; 1915, p. 46) in the Oxyaenidae. Four distinct phyla or subfamilies are represented, of which the Oxyaeninae and Palaeonictinae are retained in the family Oxyaenidae in this paper, while the Limnocyoninae and Machairoidinae are referred to the Hyaenodontidae. An attempt is made to trace the structural and functional evolution within the four groups, to determine the origin and phylogeny of each line, and to give a systematic revision.

A large part of the material examined is in the collection of the American Museum of Natural History. Other museums visited which contain specimens of this group are the Peabody Museum at Yale, the Museum of Comparative Zoology at Harvard, the Geological Museum of Princeton University, the U. S. National Museum, and the Carnegie Museum. The writer is indebted to J. J. Burke, C. L. Gazin, Walter Granger, W. K. Gregory, G. L. Jepsen, A. S. Romer, W. B. Scott, G. G. Simpson and M. R. Thorpe of the above museums for permission to study their material and for assistance in this work.

HISTORY OF THE STUDY OF THE GROUP

Charles d'Orbigny in 1836 described the trigonid of a lower molar from the Sparnacian (Lower Eocene) of Meudon, France, as "*Loutre*"; this fragment probably belongs to *Palaeonictis* and is the first specimen of the broad-skulled Pseudocreodi to be mentioned in the literature. In 1842, de Blainville named the genus *Palaeonictis*, and described and figured it from better material, but considered it to be a viverrid; it was not until after the discovery in North America of more complete material of related genera that its true affinities were recognized. The two other European forms, both from the Phosphorites of Quercy, were described by Filhol, *Thereutherium* in 1876 and "*Oxyaena*" *galliae* in 1882. His descriptions were supplemented later by Lydekker (1884), Schlosser (1887), Martin (1906) and Leche (1915).

Most of the broad-skulled Pseudocreodi occur in North America, and thus it is the paleontologists of this continent who figure most prominently in the study of the group. Leidy in 1870 described the first form, *Patriofelis ulta*. In 1872 Marsh described numerous new genera and species from the Bridger or Middle Eocene. Of the early workers, however, it was Cope who added most to our knowledge of the group. His descriptions of Lower Eocene specimens, though valuable, are not his most important contribution; for he was the first to realize the general relationships of the Creodonta, and the ancestral position they occupy relative to the fissipedes. As early as 1880 (A) he had achieved a classification which, though leaving much to be desired, was a substantial basis for further work. In 1895 in Denmark, Winge produced a fundamentally different classification of Carnivora, based on the basicranial region, on foot structure, and more especially on his theory of cusp homologies and evolution.

At the close of the nineteenth century Scott, Wortman, and Osborn produced important papers on the group. Scott in 1892 revised the classification of Cope somewhat. In 1894, Wortman produced the earliest thorough osteological description of a member of the group, and also made the first satisfactory attempt to determine adaptation. In 1901 and 1902 he made a complete study of the Marsh collection of Middle Eocene creodonts. Wortman was a strong advocate of the theory of derivation of the seals from *Patriofelis* and of the Felidae from the Palaeonictidae, two ideas now completely discredited. Osborn contributed several papers describing new forms from the Wasatch and Huerfano beds, and the first known North American Upper Eocene member of the group, whose affinities he did not correctly determine.

Matthew is the outstanding figure in the study of the group in the twentieth century. In numerous papers he improved greatly the classifications of Cope, expressed the views on the relationships of the creodonts which are now generally accepted, and described many new genera and species, as well as furnishing more complete descriptions of earlier named forms. Other descriptive papers have been written by Peterson (1919) on the Upper Eocene forms, Jepsen (1930) on specimens from the Upper Paleocene especially, and Thorpe (1923) on Middle Eocene creodonts. Important work on the stratigraphic position of these fossil mammals has been done by Teilhard de Chardin in Europe, and Granger, Osborn, Matthew and Simpson in North America.

SYSTEMATIC REVISION

Superfamily PSEUDOCREODI Matthew 1909 (327)

Carnassials $M\frac{1}{2}$ or $M\frac{2}{3}$. Ungual phalanges fissured at tip. Lumbar zygapophyses cylindrical or revolute.

This superfamily is distinguished from the Acreodi (Mesonychidae and Arctocyonidae) by the presence of specialized carnassial teeth, and from the Eucreodi (Miacidae) by the position of the carnassials in the tooth row, the cleft unguals, and the more complex lumbar zygapophyses. It includes the Oxyaenidae and Hyaenodontidae.

Family OXYAENIDAE Cope 1877 (89)

$P\frac{1}{1}$ single-rooted or absent; $P^{\underline{3}}$ with protocone progressively developed; $M\frac{1}{2}$ functioning as carnassials; $M^{\underline{2}}$ transverse or absent; $M\frac{3}{3}$ absent in all known genera; cheek tooth-row short. Jaw short and deep, with robust symphysis and short, bluntly rounded angle. Face moderately to very short; basicranial region broad; preglenoid crest present. Body robust. Sacrum lacking distinct anterior process from lateral mass. Feet pentadactyl, short and spreading, plantigrade or subplantigrade. Unguals flattened dorso-ventrally. Proximal fibular facet of tibia facing mostly ventrally. Fibulo-calcanear articulation small or usually absent. Astragalar body much flattened, with very shallowly grooved trochlear surface. Cuboid-astragalar facet large, facing rather proximo-distally.

As originally defined by Cope (1877, p. 89), this family included *Stypolophus*, *Oxyaena*, *Pterodon* and perhaps *Patriofelis*. Matthew in 1909 (p. 409, 410) included *Oxyaena*, *Patriofelis*, *Palaeonictis* and *Ambloctonus* in the Oxyaeninae, and *Limnocyon*, *Thinocyon*, *Oxyaenodon*, *Thereutherium* and *Machaeroides* in the Limnocyoninae. In 1915 (p. 42) he implied the separation of *Palaeonictis* and *Ambloctonus* from the Oxyaeninae. The family is redefined here to contain only the Oxyaeninae of Matthew's 1909 classification, subdivided as suggested in his 1915 paper.

Subfamily OXYAENINAE Wortman 1902 (116)

$M_{\overline{2}}$ larger than $M_{\overline{1}}$; $M^{\underline{1}}$ and $P^{\underline{4}}$ with elongate metastyles. Angle of jaw projecting very slightly.

This subfamily is used to include the same genera as in Wortman's 1902 paper, but is redefined to distinguish it from the Palaeonictinae instead of from the Limnocyoninae. Hay also used Oxyaeninae as a

new subfamily in August 1902, but credit for the name goes to Wortman, whose paper appeared in February, 1902.

DIPSALIDICTIDES, NEW GENUS

Genotype: *Dipsalidictis amplus* Jepsen (1930 B). Lower molars as in primitive species of *Oxyaena*, subequal in size, trigonids wider than long, and with large metaconids and talonids. $\mathrm{M}^{\underline{1}}$ very wide transversely, with short metastyle. $\mathrm{M}^{\underline{2}}$ transverse, less reduced than in *Oxyaena*. $\mathrm{P}_{\overline{1}}$ with small anterior basal cusp; $\mathrm{P}^{\underline{4}}$ relatively wide transversely, with large protocone lobe; $\mathrm{P}^{\underline{3}}$ simple, lacking protocone.

The type of the genus *Dipsalidictis* is referred to *Oxyaena*, making necessary the creation of a new genus for this species, which differs markedly in its wide $\mathrm{M}^{\underline{1}}$ with small metastyle and unreduced protocone, and in its wide $\mathrm{P}^{\underline{4}}$. It is probable that these characters are primitive, since the lower teeth, $\mathrm{M}^{\underline{2}}$ and $\mathrm{P}^{\underline{3}}$ are less progressive than in other members of the Oxyaeninae; but there is a possibility that they represent a specialization in a different direction from other members of the subfamily.

Dipsalidictides amplus (Jepsen) 1930 (B, 128, pl. 4, figures 1 and 2)

FIGURES 6, 8

Lower Eocene, Lower Gray Bull (Sand Coulee), Clark Fork Basin, Wyoming. Size small; length $\mathrm{M}_{\overline{1}-\overline{2}}$ 20.7 mm.

OXYAENA Cope 1874 (599)

Dentition, $\frac{3-2}{3-1}$, $\frac{1}{1}$, $\frac{4}{4}$, $\frac{2}{2}$, M^{2} transverse and reduced; $\mathrm{M}^{\underline{1}}$ with protocone of moderate size and metastyle not excessively elongate; $\mathrm{P}^{\underline{3}}$ with protocone absent to large. $\mathrm{M}_{\overline{2}}$ with talonid and metaconid large to moderately small, and with shear angle progressively reduced, but not paralleling jaw; $\mathrm{M}_{\overline{1}}$ considerably reduced in advanced species, its trigonid not extended antero-posteriorly. Jaw moderately short and deep. Facial region not excessively shortened, nor palate greatly widened. Body, limbs and feet slender to moderately robust.

Oxyaena platypus (Matthew) 1915 (65, figures 54–56)

FIGURES 8, 11, 14, 25B and 26A, B, E

Upper Paleocene, Clark Fork, Bighorn Basin, Wyoming. Size smallest of genus; length $\mathrm{M}_{\overline{1}-\overline{2}}$ 17.1 mm. Teeth slender.

This is the type of Matthew's genus *Dipsalidictis*, which he considered to be a member of the Limnocyoninae. But it is definitely an

oxyaenine, which differs from other primitive species of *Oxyaena* only in its smaller size.

Oxyaena aequidens Matthew 1915 (47, figure 41)

FIGURE 6

Upper Paleocene, Clark Fork, Bighorn Basin, Wyoming. Size moderate; length $M_{\overline{1}-\overline{2}}$ 26.6 mm.; teeth relatively robust; a primitive species.

Oxyaena transiens Matthew 1915 (47, figures 42–43)

Lower Eocene, Lower Gray Bull (Sand Coulee), Clark Fork Basin, Wyoming. Size small; length $M_{\overline{1}-\overline{2}}$ 22.5 mm.; slightly advanced beyond *Oxyaena platypus*.

Oxyaena gulo Matthew 1915 (53, figures 47–48)

FIGURES 5, 6, 8, 11

Lower Eocene, Lower Gray Bull (Sand Coulee) to Middle Gray Bull, Bighorn, Clark Fork and Wind River Basins, Wyoming. Size moderate; length $M_{\overline{1}-\overline{2}}$ 26–29 mm.; intermediate in specialization.

Oxyaena intermedia, NEW SPECIES

FIGURE 5

Type: Amer. Mus. No. 15183, lower and upper jaws with teeth, skull fragments and some skeletal parts.

Paratype: Amer. Mus. No. 15184, lower jaws with teeth. Both from the Lower Eocene, Middle Gray Bull, Bighorn Basin, Wyoming.

Specific characters: Size large; length $M_{\overline{1}-\overline{2}}$ 32.5–34. mm. $M^{\underline{1}}$ with protocone little reduced; $P^{\underline{3}}$ with moderately strong protocone lobe; $M_{\overline{1}}$ somewhat smaller than $M_{\overline{2}}$ ($M_{\overline{1}}/M_{\overline{2}}$ .90–.91); trigonid of $M_{\overline{2}}$ longer than wide (W/L .91–.97); talonid of $M_{\overline{2}}$ moderately large (36–39% of length of tooth); angle of shear fairly high; $P_{\overline{4}}$ rather robust.

This species includes most of the Middle Gray Bull specimens formerly referred to *Oxyaena forcipata*. Although it agrees with the latter in size, it is definitely more primitive than the typical *Oxyaena forcipata*, being of about the same stage of evolution as its smaller contemporary, *Oxyaena gulo*. It may be distinguished from both *O. lupina* and *O. forcipata* by its wider trigonids, larger talonids and metaconids on the lower molars, less reduced $M_{\overline{1}}$, larger protocone on $M^{\underline{1}}$; most of these characters result in a less perfect carnassial shear. The type specimen has been figured by Matthew (1915, figures 45–46).

Oxyaena forcipata Cope 1874 (600)

FIGURES 27, 31

Lower Eocene, Almagre and ? Largo, San Juan Basin, New Mexico; Upper Gray Bull to Lost Cabin, Bighorn Basin, Wyoming; Huerfano A, Huerfano Basin, Colorado. Size large; $M_{\overline{1}-\overline{2}}$ 31–34 mm. $M^{\underline{1}}$ with protocone considerably reduced; $P^{\underline{3}}$ with well developed protocone; $M_{\overline{1}}$ much smaller than $M_{\overline{2}}$ ($M_{\overline{1}}/M_{\overline{2}}$ .77–.86); trigonid of $M_{\overline{2}}$ longer than wide (W/L .77–.79); talonid on $M_{\overline{2}}$ considerably reduced (28–34% of length of tooth); angle of shear moderately low; $P_{\overline{4}}$ robust.

This species is redefined to include only those specimens which resemble the type in the advanced development of the carnassial shear. The distinctions from *O. intermedia* are noted above, but there are many intermediate forms. It is distinguished from *O. lupina* mostly by its larger size and greater robustness, especially of the premolars. Both the type and paratype of *O. pardalis* Matthew (1915, p. 55, figure 49) are referred to this species; their size is only slightly larger, the canine is not more robust, as Matthew stated, and the broad heel of $P_{\overline{4}}$ is by itself an unreliable character to distinguish a separate species. The type of *O. forcipata* is figured by Cope (1877, pl. XXXVI, figures 1–6).

Oxyaena lupina Cope 1874 (599)

FIGURE 6

Lower Eocene, Almagre and Largo, San Juan Basin, New Mexico; Huerfano A, Huerfano Basin, Colorado; ? Lysite, Wind River Basin, Wyoming. Size moderate; $M_{\overline{1}-\overline{2}}$ 28–29.5 mm.

This is an advanced species, distinguished from *O. forcipata* by the characters noted above. Typical specimens are all from New Mexico; the Huerfano forms (*O. huerfanensis* Osborn 1897, p. 255) are slightly larger and more advanced; the Lysite specimen (Princeton No. 13444) is slightly larger, but probably closely related. The type specimen is figured by Cope (1877, pl. XXXV, figures 1–4).

Oxyaena ultima, NEW SPECIES

FIGURES 1, 5

Type: Harvard, Mus. Comp. Zool. No. 3423, right lower jaw with $C_{\overline{1}}$ to $M_{\overline{2}}$; skeletal fragments; from the Lower Eocene, Lost Cabin, North Fork of Wind River, Wind River Basin, Wyoming.

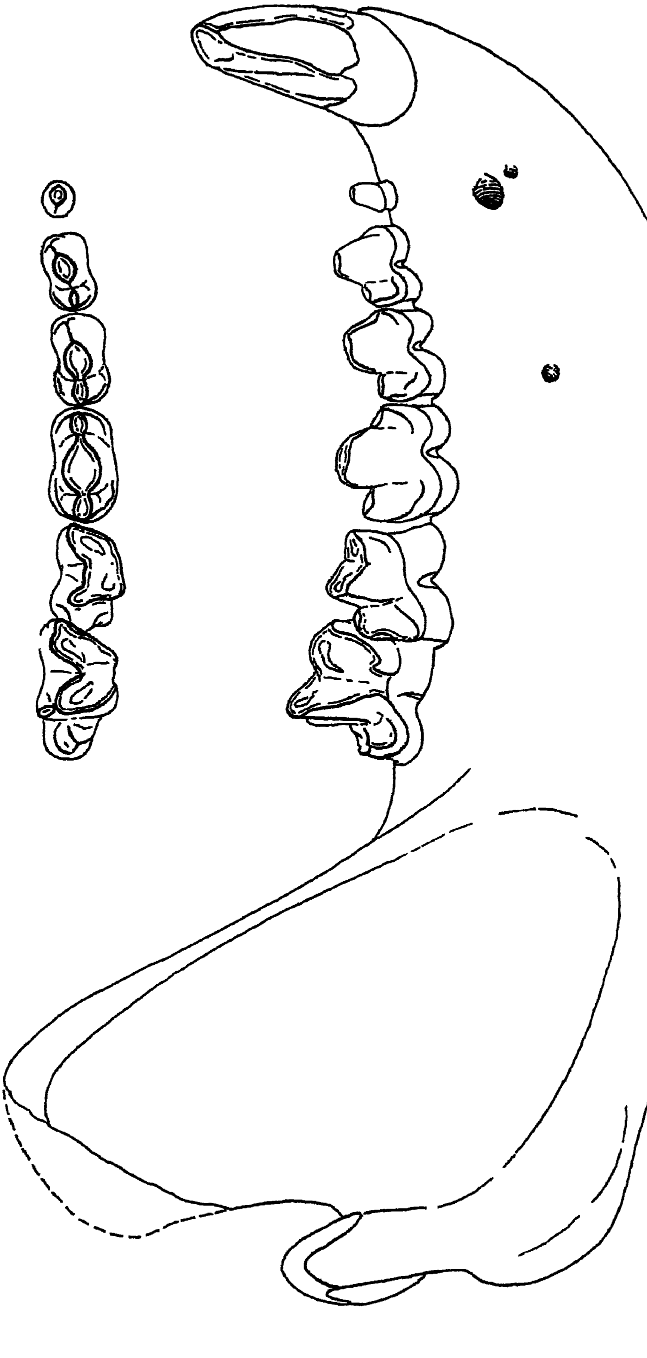


FIGURE 1. *Oxyaena ultima*, external view of lower jaw and crown view of lower cheek teeth, natural size. Type specimen, Mus Comp. Zool. No 3123

Specific characters: Size large; $M_{\overline{1}-\overline{2}}$ 32 mm.; $P_{\overline{1}}$–$M_{\overline{2}}$ 81 mm.; length $M_{\overline{2}}$ 19.8 mm. $M_{\overline{1}}$ much smaller than $M_{\overline{2}}$; trigonids of lower molars narrow, talonids rather small; metaconid of $M_{\overline{2}}$ vestigial; shear angle low; $P_{\overline{1}}$ compressed, with large anterior basal cusp.

This species is the size of *O. forcipata*, from which it differs markedly in the slender, compressed lower premolars; W/L of $P_{\overline{4}}$ is only .52, as compared to .57–.60 in *O. forcipata*. This character agrees better with *O. lupina*, of which this species may be a large derivative.

PROTOPSALIS Cope 1880 (B, 745)

$M_{\overline{2}}$ with very small talonid, vestigial metaconid, and well defined shearing surface on the enlarged paraconid and protoconid; $M_{\overline{1}}$ considerably reduced, with small metaconid closely applied to protoconid, and with trigonid cusps less drawn out antero-posteriorly than in *Patriofelis*. $M^{\underline{1}}$ with protocone small, but larger than in *Patriofelis*, and with external cusps less elongate than in *Patriofelis;* $P^{\underline{3}}$ with large protocone. Jaw deep.

Protopsalis has not quite attained the *Patriofelis* stage of carnassial construction, but is intermediate between the latter genus and *Oxyaena*. Because of this fact, it is retained here as a distinct genus.

Protopsalis tigrinus Cope 1880 (B, 745)

FIGURE 6

Lower Eocene, Lost Cabin, Wind River Basin, Wyoming. Size large; length $M_{\overline{2}}$ 25 mm. For illustrations of type, see Cope 1884 (A, pl. XXVb, figures 1–7).

PATRIOFELIS Leidy 1870 (10)

Dentition, $\frac{?}{2-3}$, $\frac{1}{1}$, $\frac{3}{3}$, $\frac{1}{2}$. $M^{\underline{2}}$ absent; $M^{\underline{1}}$ with protocone vestigial, and with external cusps, especially the metastyle, greatly elongate; $P^{\underline{3}}$ with large protocone lobe; $P^{\underline{2}}$ two-rooted, but much widened internally; $P\frac{1}{1}$ absent. $M_{\overline{2}}$ with talonid and metaconid absent or vestigial, and with elongate shearing surface approximately parallel to jaw axis; $M_{\overline{1}}$ with trigonid cusps flattened transversely and drawn out antero-posteriorly, and with single-cusped, shearing talonid; $P_{\overline{3}-\overline{4}}$ with large, distinct anterior basal cusps. Jaw short and deep. Skull very short and broad. Body and limbs robust; feet very short and spreading.

Patriofelis coloradensis Matthew 1909 (in Osborn, 1909, 96)

Middle Eocene, Huerfano B, Huerfano Basin, Colorado. Smallest of genus; $P_{\overline{2}}$–$M_{\overline{2}}$ 60 mm.; $M_{\overline{1}-\overline{2}}$ approximately 26 mm.

This specimen was first described by Osborn (1897, p. 256) as *P. ulta*, then distinguished by Matthew (1909, p. 96) as this species, and

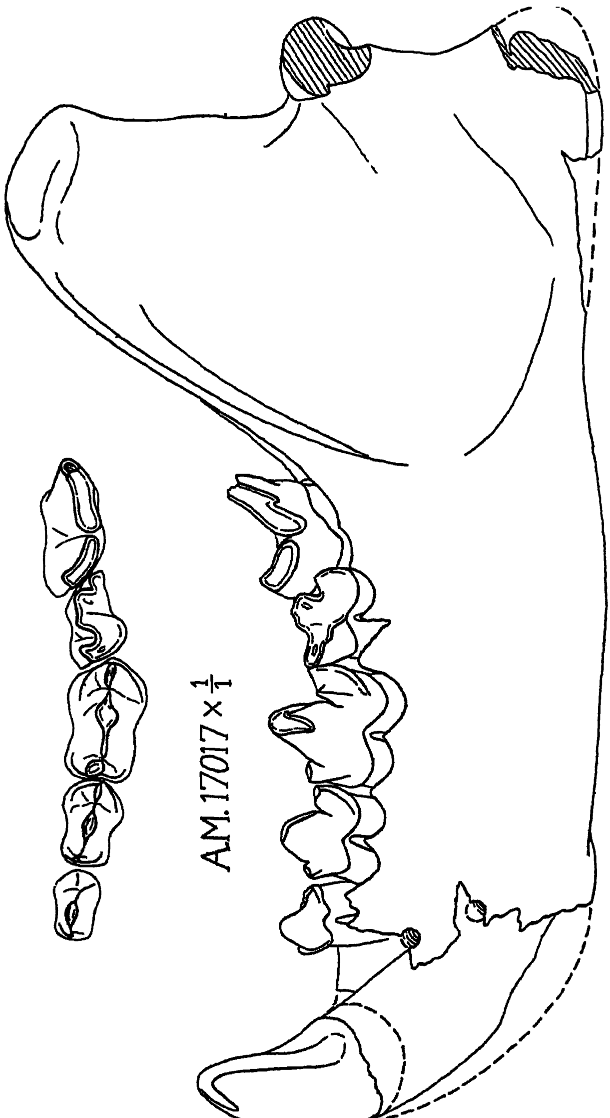


FIG *Patriofe* xternal vi lower jaw and crown view
Type spe , Amer. Mus No. 17017.

finally referred to *Ambloctonus* by Matthew in 1915 (p. 62). It certainly is distinct from *P. ulta* because of its small size and other char-

acters. The absence of $M_{\overline{1}}$ and the worn condition of the teeth give rise to the confusion as to its proper generic reference. In the very broad, robust lower premolars this specimen may resemble *Ambloctonus* slightly more than *Patriofelis*, but these teeth are very similar in the two genera. $M_{\overline{2}}$ appears relatively small for *Patriofelis*, but this is due largely to the fact that it is greatly worn; in details of its construction it is closer to *Patriofelis*. The jaw gives the most conclusive evidence of relationship with *Patriofelis;* the form of the insertion areas for the pterygoid and temporalis muscles are exactly as in other species of the latter genus, and the angle is very short as in all Oxyaeninae, whereas it projects much more in the Palaeonictinae. The type, and only specimen, is figured by Osborn (1900, figure 8).

Patriofelis compressa, NEW SPECIES

FIGURE 2

Type: Amer. Mus. No. 17017; left lower jaw, nearly complete, with $C_{\overline{1}}$–$M_{\overline{2}}$; right $P_{\overline{4}}$ and $C_{\overline{1}}$; limb fragments. From the Middle Eocene, Huerfano B, Big Sand Draw, 3 miles northwest of Gardner, Huerfano Basin, Colorado.

Specific characters: Size fairly small; $P_{\overline{2}}$–$M_{\overline{2}}$ 65 mm.; $M_{\overline{1}-\overline{2}}$ 28 mm.; length $M_{\overline{2}}$ 17.4 mm. $P_{\overline{4}}$ shorter than $M_{\overline{2}}$; lower premolars and canine less robust than in other species of the genus.

This species is sharply distinguished from all the others in the genus by its relatively slender premolars. It is smaller than *P. ferox* and *P. ulta*, and slightly larger than *P. coloradensis*.

Patriofelis ulta Leidy 1870 (10)

Middle Eocene, Bridger B, Bridger Basin, Wyoming; ? "Lower Bridger," Wind River Basin, Wyoming. Size moderately large; $P_{\overline{2}}$–$M_{\overline{2}}$ 75.5 mm.; $M_{\overline{1}}$–$_{\overline{2}}$ 32.2 mm.; jaw shallow; premolars robust; $P_{\overline{4}}$ larger than $M_{\overline{2}}$. (Figured by Leidy, 1873, pl. II, figure 10.)

Patriofelis ferox (Marsh) 1872 (B, 202)

FIGURES 5, 6, 8, 11, 16, 19, 20, 23, 24B, 25C, 26C, 27, 28B, 29B, 30B, 31

Middle Eocene, Bridger C–D, Bridger Basin; Washakie A, Washakie Basin; ? "Bridger C," Wind River Basin, Wyoming. Size largest of genus; $P_{\overline{2}}$–$M_{\overline{2}}$ 78–84 mm.; $M_{\overline{1}-\overline{2}}$ 35–36 mm. Jaw very deep and heavy; premolars and $C_{\overline{1}}$ robust; $P_{\overline{4}}$ about equal to $M_{\overline{2}}$ in length.

Synonyms are *Limnofelis ferox* Marsh 1872 (B, p. 202), *Oreocyon latidens* Marsh 1872 (C, p. 406), and *Aelurotherium* Adams 1896 (p. 442). That *Aelurotherium* is the milk dentition of *P. ferox* is confirmed by a specimen in the U. S. National Museum (No. 13318) with $DP_{\overline{3}-\overline{4}}$ and $M_{\overline{1}}$ erupting. The Wind River Basin individual

(Wood, Seton & Hares, 1936, p. 394) is slightly smaller, but otherwise close to typical specimens. This species is completely described by Wortman (1894) and Matthew (1909, p. 417–432).

SARKASTODON Granger 1938 (1)

Dentition, $\frac{2}{1}$, $\frac{1}{1}$, $\frac{3}{3}$, $\frac{1}{2}$. Cheek teeth much as in *Patriofelis;* M^1 excessively shearing, with vestigial protocone; premolars robust; P^2 probably with internal root; lower premolars extremely wide, with small anterior basal cusps; canines and I^3 very large and robust; I^2 vestigial and I^1 absent; only a single, small lower incisor. Jaw very short and deep. Skull very short, broad and robust.

Sarkastodon mongoliensis Granger 1938 (1)

Upper Eocene, Irdin Manha formation, Inner Mongolia. Size very large; P_3–M_2 160–164 mm.; M_{1-2} 76–77 mm. This is the largest known carnivorous mammal with the exception of the mesonychid, *Andrewsarchus.*

Subfamily PALAEONICTINAE, NEW

M_2 smaller than M_1; M^1 and P^4 with short metastyle; angle of jaw bluntly rounded, but projecting considerably.

This group resembles the Oxyaeninae in skull and skeletal characters, but differs in the teeth, the carnassial adaptation being less pronounced, and the posterior shearing teeth being reduced in size. *Palaeonictis* and *Ambloctonus* have been referred to a separate family, Ambloctonidae by Cope (1877, p. 89), or Palaeonictidae by Osborn (in Osborn & Wortman, 1892, p. 104), to subfamily Palaeonictidini of the family Palaeonictidae by Winge (1924, p. 177), and to the subfamily Oxyaeninae of the family Oxyaenidae by Matthew (1909, p. 409) and others.

DIPSALODON Jepsen 1930 (A, 524)

Lower dentition, ?, 1, 4, 2. M_1 very slightly larger than M_2; lower molars primitive, with unreduced metaconid, no carnassial specialization, and large basined heels; hypoconid, hypoconulid and entoconid distinct on M_1; lower premolars and C_1 robust; P_4 with large anterior basal cusp; jaw deep and strong. A primitive oxyaenid, not far different from early species of *Oxyaena* in its lower teeth, but showing tendencies towards *Palaeonictis.*

Dipsalodon matthewi Jepsen 1930 (A, 524)

FIGURES 6, 11

Upper Paleocene, Uppermost Clark Fork, Clark Fork Basin, Wyoming. Size rather large; P_1–M_2 approximately 81 mm.; M_{1-2}

27.5 mm. Amer. Mus. No. 16068 from the same horizon, decribed by Matthew (1915, p. 47) as "? *Oxyaena* sp. innom.", is referred here doubtfully. It includes much worn upper teeth of approximately the same size as *D. matthewi;* $P^{\underline{4}}$ and $M^{\underline{1}}$ have relatively short parastyles and metastyles, in which they resemble *Palaeonictis.*

PALAEONICTIS Blainville 1842 (79)

Dentition, $\frac{3}{3}$, $\frac{1}{1}$, $\frac{4}{4}$, $\frac{2}{2}$. $M_{\overline{2}}$ considerably reduced, of tuberculo-sectorial type, with metaconid moderate to vestigial, paraconid and protoconid not much enlarged, talonid little reduced; trigonid of $M_{\overline{1}}$ not elongate antero-posteriorly; lower premolars robust, with large anterior basal cusp on $P_{\overline{4}}$; $M^{\underline{2}}$ vestigial; jaw relatively deep and robust.

This genus is distinguished from *Dipsalodon* by the greater reduction of $M_{\overline{2}}$ and its metaconid, and from *Ambloctonus* by the tuberculo-sectorial form of $M_{\overline{2}}$, its large talonid, and by the relatively short trigonid of $M_{\overline{1}}$.

Palaeonictis gigantea Blainville 1842 (76–79, pl. XIII)

Lower Eocene (Sparnacian), Lignites de Muirancourt, near Noyon, and Conglomérat de Meudon, near Paris, France. Size smaller than *P. occidentalis;* $M_{\overline{1}-\overline{2}}$ 19–21 mm.; $M_{\overline{2}}$ less reduced than in *P. occidentalis* ($M_{\overline{1}}/M_{\overline{2}}$ 1.14–1.26); $M_{\overline{2}}$ with large metaconid and three distinct talonid cusps.

This species is very close to *P. occidentalis* of Wyoming, but may be slightly more primitive. The typical specimens are from the Lignites de Muirancourt; probably related is a trigonid of a lower molar from the Conglomérat de Meudon, originally described by d'Orbigny (1836, p. 287) as "*Loutre.*"

Palaeonictis occidentalis Osborn 1892 (30)

FIGURES 5, 6, 9, 11, 14, 16

Lower Eocene, Lower Gray Bull (Sand Coulee) to Middle Gray Bull, Bighorn Basin, Wyoming. Size moderate; $M_{\overline{1}-\overline{2}}$ 23.5–24.5; $M_{\overline{1}}/M_{\overline{2}}$ 1.25–1.45; metaconid of $M_{\overline{2}}$ moderate to vestigial.

Ambloctonus priscus of Matthew (1915, p. 60) must be referred here. The type specimens differ from the type of *P. occidentalis* in several characters, but they do not warrant even a specific separation. The canines of *A. priscus* are smaller, but this is a variable character, perhaps sexual, in this group. $M^{\underline{2}}$ is a small, transverse, two-rooted tooth in the type of *A. priscus,* whereas it is a single-rooted nubbin in the type of *P. occidentalis;* but such a variation is to be expected in a vestigial tooth, and is exceeded in a single species of cat, *Felis concolor.*

$M_{\overline{2}}$ has a vestigial metaconid and moderately distinct talonid cusps in *A. priscus*, but other specimens show all the intergradations to the type of *P. occidentalis* where the metaconid is moderately strong and the talonid cusps are not clearly separated. Other differences in the cingula and accessary cusps of the lower premolars are clearly individual variations. On the other hand, the two types agree closely in size, tooth pattern, and even in the surface markings on the skull.

AMBLOCTONUS Cope 1875 (A, 7)

Dentition, $P\frac{?}{4}$, $M\frac{2}{2}$, $M_{\overline{2}}$ considerably smaller than $M_{\overline{1}}$, with talonid small or lacking, metaconid absent, and with protoconid and paraconid enlarged and connected by a curved shearing ridge; $M_{\overline{1}}$ with trigonid cusps elongate and arranged in a crescent, and with large, basined talonid; lower premolars very broad; $P_{\overline{4}}$ with large anterior basal cusp; $M^{\underline{2}}$ probably present, but vestigial; jaw short and deep.

Ambloctonus sinosus Cope 1875 (A, 8)

FIGURES 6, 11

Lower Eocene, "Wasatch" (=? Largo), San Juan Basin, New Mexico. Size moderate; length $M_{\overline{1}}$ 15.5 mm.; $M_{\overline{2}}$ 12.3 mm.; $M_{\overline{2}}$ with small talonid; lower teeth robust. (Figured by Cope 1877, pl. XXXIII, figures 1–10.)

Ambloctonus hyaenoides Matthew 1915 (61, figures 50, 52)

FIGURE 6

Lower Eocene, Largo, San Juan Basin, New Mexico. Size about that of *A. sinosus;* length $M_{\overline{1}}$ 16 mm.; $M_{\overline{2}}$ 12.5 mm.; $M_{\overline{2}}$ with talonid practically absent; lower teeth narrower and less robust than in *A. sinosus.*

This species includes as paratype one of the specimens referred by Cope to *A. sinosus* (1877, pl. XXXIII, figure 11).

Ambloctonus major, NEW SPECIES

Type: Amer. Mus. No. 16853; left lower jaw fragment with $DP_{\overline{4}}$ and $M_{\overline{1}}$: fromt he Lower Eocene, Lost Cabin, Bighorn Basin, Wyoming.

Specific characters: Size larger than *A. hyaenoides;* length $M_{\overline{1}}$ 19 mm.; entoconid of $M_{\overline{1}}$ larger than in *A. hyaenoides.*

This specimen was referred by Matthew (1915, p. 61, figure 53) to *A. hyaenoides*, but is separated because of its distinctly larger size.

PAROXYAENA Martin 1906 (598)

Dentition, $\frac{3}{0}$, $\frac{1}{1}$, $\frac{4}{4}$, $\frac{?}{2}$. $I^{\underline{3}}$ much enlarged, $I^{\underline{2}}$ reduced, $I^{\underline{1}}$ absent; $P^{\underline{2}}$ probably lacking protocone; $P^{\underline{3-4}}$ three-rooted, with large, wide protocone lobes, small metastyle and anterior cusps; face very short.

Paroxyaena galliae (Filhol) 1882 (120)

FIGURE 5

Upper Eocene, Phosporites de Quercy, Mouillac (near Caylux) and Escamps (near Lalbenque), France. Size rather large; P^{1-4} 57 mm.; length P^4 17 mm.

This form was described originally as a member of the genus *Oxyaena* by Filhol in 1882. Martin in 1906 referred it to a separate genus, *Paroxyaena*, because he considered its similarity to *Oxyaena* to be due to convergence. Its resemblance to *Oxyaena*, however, is not very close. P^4, with its short metastyle, small anterior cusp, and wide protocone lobe resembles the Palaeonictinae more closely. The incisors and P^1 resemble both the Oxyaeninae and Palaeonictinae. It is placed in the latter subfamily only provisionally. (Figured by Filhol 1884, pl. VII, figures 6 and 7.)

Family HYAENODONTIDAE Leidy 1869 (38)

$P\frac{1}{1}$ two-rooted, except in some specialized genera; P^3 lacking distinct protocone; $M\frac{1}{2}$ or $M\frac{2}{3}$ functioning as main carnassials; $M\frac{3}{3}$ present or absent; cheek tooth row moderate to long. Jaw long and shallow to moderately short and deep, with symphysis weak to fairly robust, and angle long, slender, projecting and upcurved at tip. Face long to moderately short; basicranial region narrow to moderately wide; no preglenoid crest. Body more slender than in Oxyaenidae. Sacrum with distinct anterior process from lateral mass. Feet pentadactyl, long and slender to moderately short and broad, digitigrade to subplantigrade. Ungual phalanges laterally compressed. Proximal fibular facet of tibia facing mostly laterally. A well developed fibulo-calcanear articulation. Astragalar body moderately deep; trochlear surface shallowly grooved. Cuboid-astragalar facet small or absent, facing mostly mesio-laterally.

The definition of the family is modified here so as to include the Limnocyoninae and Machaeroidinae, as well as the more typical hyaenodontids, the Proviverrinae and Hyaenodontinae.

Subfamily LIMNOCYONINAE Wortman 1902 (117)

Carnassial teeth $M\frac{1}{2}$; $M\frac{3}{3}$ lost early; C_1 not reduced and C^1 not enlarged. Skull relatively short and broad. Jaw lacking ventral flange anteriorly.

This group is distinguished from the Machaeroidinae by the absence of any sabre-tooth specializations, and from the Proviverrinae and Hyaenodontinae by the position of the carnassials and the breadth of

the skull. The reason for the inclusion of this group in the Hyaenodontidae will be discussed below.

PROLIMNOCYON Matthew 1915 (67)

Dentition, $\frac{?}{3}$, $\frac{?}{1}$, $\frac{?\,4}{4}$, $\frac{3}{3}$. $M\frac{3}{3}$ small or vestigial; $M^{\underline{2}}$ with distinct metacone and fairly short parastyle; $M^{\underline{1}}$ wide transversely, with unreduced protocone; $P^{\underline{3}}$ three-rooted; $M_{\overline{1}-\overline{2}}$ subequal or $M_{\overline{1}}$ slightly reduced; trigonid of $M_{\overline{2}}$ about as wide as long; $P_{\overline{1}}$ two-rooted or with roots connate. Jaw long and shallow. Skull moderately narrow, with facial region long.

This is the most primitive genus of the subfamily, approaching very close to the Proviverrinae.

Prolimnocyon atavus Matthew 1915 (68, figures 57–61)

FIGURES 7, 10, 12, 15, 17

Lower Eocene, Lower Gray Bull (Sand Coulee) to Upper Gray Bull and ? Lysite, Bighorn Basin, Wyoming; ? Almagre, San Juan Basin, New Mexico. Size small; $M_{\overline{1}-\overline{3}}$ 13–16.5 mm.; $M_{\overline{3}}$ small, with two roots distinct or partly connate; jaw shallow.

Prolimnocyon robustus Matthew 1915 (70, figures 57 and 62)

Lower Eocene, Middle Gray Bull, Bighorn Basin, Wyoming. Size large; $M_{\overline{1}-\overline{3}}$ approximately 21 mm.; $M_{\overline{3}}$ two-rooted, less reduced than in *P. atavus;* jaw deeper than in *P. atavus.*

Prolimnocyon antiquus Matthew 1915 (70, figure 63)

FIGURE 12

Lower Eocene, Lost Cabin, Wind River Basin, Wyoming. Size that of *P. atavus;* $M_{\overline{1}-\overline{3}}$ 16 mm.; $M_{\overline{3}}$ one-rooted, vestigial; jaw shallow.

LIMNOCYON Marsh 1872 (A, 126)

Dentition, $\frac{3\,2}{3}$, $\frac{1}{1}$, $\frac{4}{4}$, $\frac{2}{2}$. $M\frac{3}{3}$ absent; $M^{\underline{2}}$ transverse, with metacone vestigial and parastyle elongate; $M^{\underline{1}}$ with protocone reduced slightly; $P^{\underline{3}}$ two-rooted, lacking protocone; $M_{\overline{1}}$ somewhat smaller than $M_{\overline{2}}$; trigonid of $M_{\overline{2}}$ narrower than long; $P\frac{1}{1}$ two-rooted. Jaw deep, with robust symphysis. Skull moderately broad, with strong sagittal and occipital crests. Body and limbs fairly robust; feet spreading and plantigrade. Size moderate.

Limnocyon verus Marsh 1872 (A, 126)

FIGURES 5, 7, 12, 17, 26D, 31

Middle Eocene, Lower and Upper Bridger, Bridger Basin, Wyoming. Length $M_{\overline{1}-\overline{3}}$ 16.5–19 mm.; $I^{\underline{3}}$ present; vertical ridges on pre-

molars and canines faint; nasals not elongate. Limbs not especially robust.

As shown by Wortman (1902, p. 197), *L.* (*Telmatocyon*) *riparius* is a synonym. See Matthew, 1909 (text-figures 53–58; pl. XLIV, figure 1) for illustrations of this species.

Limnocyon potens Matthew 1909 (447)

FIGURES 5, 10, 15, 28, 29

Upper Eocene, Washakie B, Washakie Basin, Wyoming; Uinta B, Uinta Basin, Utah. Length $M_{\overline{1}-\overline{2}}$ 20.5–22.5 mm.; $I^{\underline{3}}$ absent; strong vertical ridges on canines and premolars.

There is little doubt that *L. douglassi* Peterson (1919, p. 45, pl. XXXIV, figures 11–14) from the Uinta Basin belongs to this species. It agrees very closely in size and in other characters; $P_{\overline{1}}$ is relatively larger than in the type of *L. potens*, but this is a variable feature in *Limnocyon.*

THINOCYON Marsh 1872 (B, 204)

Similar to *Limnocyon* except for the shallow jaw, weak skull crests, smaller size and more slender proportions, and sub-digitigrade feet.

This group is very closely related to *Limnocyon*, and is retained as a distinct genus only because of its sub-digitigrade, more cursorial adaptation. Most of the differences are directly correlated with the smaller size of *Thinocyon.* The species are not clearly marked because of the large number of intermediate forms and the great variability of the characters in which they differ.

Thinocyon mustelinus Matthew 1909 (461)

Middle Eocene, Bridger B, Bridger Basin, Wyoming. Size very small; $M_{\overline{1}-\overline{2}}$ 10–11 mm.; trigonid of $M_{\overline{2}}$ narrow; premolars simple and crowded; $P_{\overline{1}}$ two-rooted; jaw very shallow.

Thinocyon velox Marsh 1872 (B, 204)

FIGURES 15, 17–21, 23A, 30A, 31

Middle Eocene, Bridger B, Bridger Basin, Wyoming. Size slightly larger than *T. mustelinus;* $M_{\overline{1}-\overline{2}}$ 11.5–12.5 mm.; trigonid of $M_{\overline{2}}$ relatively wide; premolars simple and usually well spaced; $P_{\overline{1}}$ two-rooted; jaw shallow. (Figured by Matthew 1909, text-figures 59–61, pl. XLIV, figures 2–4.)

Thinocyon medius (Wortman) 1902 (204, figures 81–82)

FIGURES 5, 7, 10, 12, 24A, 25A

Middle Eocene, Upper Bridger, Bridger Basin, Wyoming. Size largest of genus; $M_{\overline{1}-\overline{2}}$ 13–14.5 mm.; $P_{\overline{4}}$ and usually $P_{\overline{3}}$ with well

developed anterior basal cusp; $P_{\overline{1}}$ two-rooted; jaw relatively deeper than in the other species. There are many intermediate forms to *T. velox*.

Thinocyon cledensis Matthew 1909 (460)

Middle Eocene, Washakie A, Washakie Basin, Wyoming. Size of *T. velox;* $M_{\overline{1-3}}$ 12.5 mm.; premolars long and narrow, lacking distinct anterior basal cusps; $P_{\overline{1}}$ one-rooted; jaw shallow. This species is advanced in the one-rooted first premolar.

OXYAENODON Matthew 1899 (49)

Dentition, $\frac{3}{3}, \frac{1}{1}, \frac{4}{1}, \frac{2}{2}$. $M^{\underline{2}}$ transverse and reduced; $M^{\underline{1}}$ broader than long; $P^{\underline{3}}$ two-rooted, with small inner bulge, but no distinct protocone; lower molars with reduced metaconid, and with some elongation of the paraconid-protoconid shear; lower premolars robust and simple; $P\frac{1}{1}$ two-rooted. Jaw thick and shallow, with bluntly rounded chin. Skull short and broad.

The form of the jaw and the broad skull are especially characteristic. The generic name was first used by Matthew in April 1899 (p. 49) in a list with a reference to a figured specimen; it was first defined by Wortman in June 1899 (p. 145).

Oxyaenodon dysodus Matthew 1899 (49)

Upper Eocene, Uinta B, Uinta Basin, Utah. Length $M_{\overline{1-3}}$ 20 mm.; jaw less abruptly rounded than in *O. dysclerus*. This form was first described by Osborn in 1895 (p. 78, figure 3) as "? *Hyaenodon.*" It was referred by Matthew in 1899 (p. 49) to this genus and species.

Oxyaenodon dysclerus Hay 1902 (759)

FIGURES 5, 7, 10, 12, 15, 17, 27

Upper Eocene, Uinta C, Uinta Basin, Utah. Size smaller; $M_{\overline{1-3}}$ 18.3 mm.; chin more abruptly rounded. Originally described by Wortman in 1899 (p. 145, figure 3) as *O. dysodus*, but renamed by Hay in 1902.

THEREUTHERIUM Filhol 1876 (289)

Dentition, $\frac{3}{3}, \frac{1}{1}, \frac{4}{1}, \frac{2}{2}$. $M^{\underline{2}}$ transverse and much reduced; $M^{\underline{1}}$ with elongate metastyle and reduced protocone; $P^{\underline{3}}$ two-rooted, lacking protocone; lower molars subequal, specialized for shearing; metaconid absent; protoconid and paraconid elongate to form shearing blade; talonid reduced on $M_{\overline{3}}$; lower premolars simple; $P\frac{1}{1}$ one-rooted, small. Jaw thick and shallow.

This genus approaches the specialization of the advanced Oxyaeninae, but its relationship with the Limnocyoninae is indicated by the

unreduced M_1, the arrangement of the lower incisors, the two-rooted $P^{\underline{2}}$ lacking protocone, shallow jaw with long, slender angle, small size and other characters. It may represent a separate line, derived from the Proviverrinae, and paralleling the Limnocyoninae.

Thereutherium thylacodes Filhol 1876 (289)

FIGURES 5, 7, 10, 12, 15

Upper Eocene, Phosphorites de Quercy, Caylux, Escamps (near Lalbenque) and Mouillac, France. Size very small; $M_{\overline{1}-\overline{2}}$ 7–8 mm.

Subfamily MACHAEROIDINAE Matthew 1909 (330)

Carnassial teeth $M\frac{1}{2}$; $M\frac{2}{3}$ absent; $C_{\overline{1}}$ reduced and, by inference $C^{\underline{1}}$ enlarged; jaw developing ventral flange anteriorly.

The Machaeroidinae are an offshoot of the Limnocyoninae showing a remarkable parallelism to the true sabre-toothed cats (Machaerodontinae). Matthew in 1909 merely suggested the subfamily name and retained *Machaeroides* in the Limnocyoninae, but the discovery of the more specialized genus, *Apataelurus*, makes the separation of this group advisable.

MACHAEROIDES Matthew 1909 (461)

Lower dentition, 2 or 3, 1, 4, 2. Lower molars with elongate paraconid-protoconid shear nearly parallel to jaw, and reduced metaconid; talonid of $M_{\overline{2}}$ very small; $P_{\overline{3}-\overline{1}}$ elongate and much compressed; $P_{\overline{1}}$ two-rooted or with roots partially united; moderate $C_{\overline{1}}$–$P_{\overline{1}}$ diastema; $C_{\overline{1}}$ small; $I_{\overline{3}}$ large; $I_{\overline{2}}$ small; $I_{\overline{1}}$ may be absent; jaw thin and moderately deep, flaring laterally at canine, and lacking ventral flange anteriorly; chin deep, nearly vertical.

The jaw of *Machaeroides* resembles that of *Felis*, and is not truly "sabre-tooth."

Machaeroides eothen Matthew 1909 (462, figures 48, 71)

FIGURES 5, 7, 13

Middle Eocene, Bridger B–C, Bridger Basin, Wyoming. Length $M_{\overline{1}-\overline{2}}$ 16 mm. The typical specimens are from Bridger B. Amer. Mus. Nat. Hist. 12083 from Bridger C is somewhat larger ($M_{\overline{1}-\overline{2}}$ 18 mm.) and has the two roots of $P_{\overline{1}}$ united; it may be considered an advanced variant.

APATAELURUS Scott 1937 (455)

Lower dentition, ? 2, 1, 4, 2. $M_{\overline{2}}$ large, with shearing blade similar to that of *Patriofelis*, with vestigial talonid and no metaconid; $M_{\overline{1}}$ much reduced, but shearing, with small metaconid and talonid; $P_{\overline{1}}$ slender and compressed, with large, distinct anterior basal cusp;

anterior premolars very small; P_1 one-rooted; long $C_{\overline{1}}$–P_1 diastema; $C_{\overline{1}}$ very small. Jaw as in *Machaerodus* or *Hoplophoneus*, with low condyle, reduced coronoid and deep anterior ventral flange.

Apataelurus is a remarkable parallel of the true sabre-tooth cats, and was probably derived from *Machaeroides*.

Apataelurus kayi Scott 1937 (455)

FIGURES 5, 7, 13

Upper Eocene, Uinta B, Uinta Basin, Utah. Length $M_{\overline{1}-\overline{2}}$ 30 mm.

Subfamilies PROVIVERRINAE Matthew and HYAENODONTINAE Matthew

These are the long-faced, narrow-skulled Pseudocreodi, with carnassials $M\frac{2}{3}$. They are not within the scope of this paper.

NOTE ON DIDYMOCONUS AND ARDYNICTIS

Ardynictis and *Didymoconus* of the Oligocene of Mongolia were considered by Matthew and Granger (1924, p. 3; 1925, p. 3) to be specialized derivatives of the Oxyaenidae, largely because they had only two molars above and below, and possessed short, heavy jaws with stout canines and massive symphyses. These genera, however, are fundamentally different from the broad-skulled Pseudocreodi in the following respects: $P\frac{4}{4}$ are very molariform, a condition not even approached in any oxyaenid; $M^{\underline{1}}$ has a small metastyle, well separated paracone and metacone, and develops a peculiar hypocone placed internal as well as posterior to the protocone; in all the broad-skulled Pseudocreodi the metastyle is elongate, the paracone and metacone are closely appressed, and the postero-internal region of the tooth is reduced, rather than extended by the development of a hypocone. $M^{\underline{2}}$ is less transverse, and has a shorter parastyle and larger metacone than in any oxyaenid or limnocyonine. $M_{\overline{1}}$ is not reduced, as is invariably the case in the Pseudocreodi. The lower molars have a large, distinct metaconid and much reduced paraconid, whereas, the paraconid is always enlarged and the metaconid reduced even in the earliest Pseudocreodi.

From the above facts, it appears highly improbable that *Didymoconus* and *Ardynictis* are related to the Pseudocreodi. If they are Carnivora, as the large canines and heavy jaw suggest, they are quite distinct from any known family of Creodonta or Fissipedia. It is possible that they were derived from some member of the Paleocene Triisodontinae, which approach them more closely in tooth construction.

GEOLOGICAL AND GEOGRAPHICAL DISTRIBUTION

The distribution of the broad-skulled Pseudocreodi is shown in FIGURES 3 and 4. The group is found largely in North America, and probably originated on that continent, since the earliest forms occur there. The Oxyaenidae make their first appearance in the Upper Paleocene of Wyoming, with representatives of both subfamilies known. During the Lower Eocene, the genus *Oxyaena* shows a rapid evolution in western North America, and in the Middle Eocene gives way to its descendant, *Patriofelis*. The giant *Sarkastodon*, the last of the Oxyaeninae, occurs in the Upper Eocene of Mongolia. It is one of many forms in the Irdin Manha formation which shows the close connection of North America and Asia in the Upper Eocene after a long period of separation.

The genus *Dipsalodon* of the Upper Paleocene of Wyoming is the earliest known member of the Palaeonictinae. It is succeeded in the early Lower Eocene by *Palaeonictis*, which occurs in both Europe and North America. Although the French species is perhaps more primitive than the North American, it migrated probably from North America during this period when the continents were closely connected. In North America, *Palaeonictis* gave rise to *Ambloctonus* and then the line died out at the end of the Lower Eocene; in Europe, it is possible that the subfamily persisted until the Upper Eocene and gave rise to *Paroxyaena* of the Phosphorites of Quercy.

The Limnocyoninae are mostly North American. Primitive members of the group (*Prolimnocyon*) appear in the Lower Eocene of Wyoming, and in the Middle Eocene the species are more varied and numerous. This is the time that their specialized offshoots, the Machaeroidinae, make their appearance. In the Upper Eocene, the Limnocyoninae are reduced in numbers in North America, and disappear before the end of the period. Little is known of the history of the group in Europe; it is possible that they never reached that continent and that *Thereutherium* is a separate offshoot of the Proviverrinae and the result of a parallel evolution. On the other hand, some primitive limnocyonine may have reached Europe when it was connected with North America in the Lower Eocene, and *Thereutherium* may have evolved from that form during the Middle and early Upper Eocene when the two continents were separated.

Epoch		Bridger Basin, Wyo.	Wind River Basin, Wyo.	Washakie Basin, Wyo.
Eocene	Upper	BRIDGER E		WASHAKIE B *Limnocyon potens*
	Middle	BRIDGER C-D *Patriofelis ferox* *Limnocyon verus* *Thinocyon medius* *Machaeroides eothen* (var.)	"BRIDGER C" *Patriofelis cf. ferox*	WASHAKIE A *Patriofelis ferox* *Thinocyon cledensis*
		BRIDGER B *Patriofelis ulta* *Limnocyon verus* *Thinocyon velox* " *mustelinus* *Machaeroides eothen*		
				Huerfano Basin, Colo.
		BRIDGER A	"BRIDGER A" *Patriofelis cf. ulta*	HUERFANO B *Patriofelis coloradensis* " *compressus*
		Bighorn Basin, Wyo.		
	Lower	"LOST CABIN" *Oxyaena forcipata* (?) *Ambloctonus major*	LOST CABIN *Oxyaena ultima* *Protopsalis tigrinus* *Prolimnocyon antiquus*	HUERFANO A *Oxyaena forcipata* " *lupina* (adv. var.)
		"LYSITE" *Oxyaena forcipata* *Prolimnocyon atavus* (?)	LYSITE *Oxyaena cf. lupina*	
		UPPER GRAY BULL *Oxyaena forcipata* *Prolimnocyon atavus*		
		MIDDLE GRAY BULL *Oxyaena gulo* " *intermedia* *Palaeonictis occidentalis* *Prolimnocyon atavus* " *robustus*		
		LOWER GRAY BULL (SAND COULEE) *Oxyaena transiens* " *gulo* *Dipsalidictides amplus* *Palaeonictis occidentalis* *Prolimnocyon atavus*	"LOWER GRAY BULL" *Oxyaena gulo*	
Upper Paleoc.		CLARK FORK *Oxyaena platypus* " *aequidens* *Dipsalodon matthewi*		

FIGURE 3. Geological and geographical distribution of the broad-skulled Pseudocreodi (Part I).

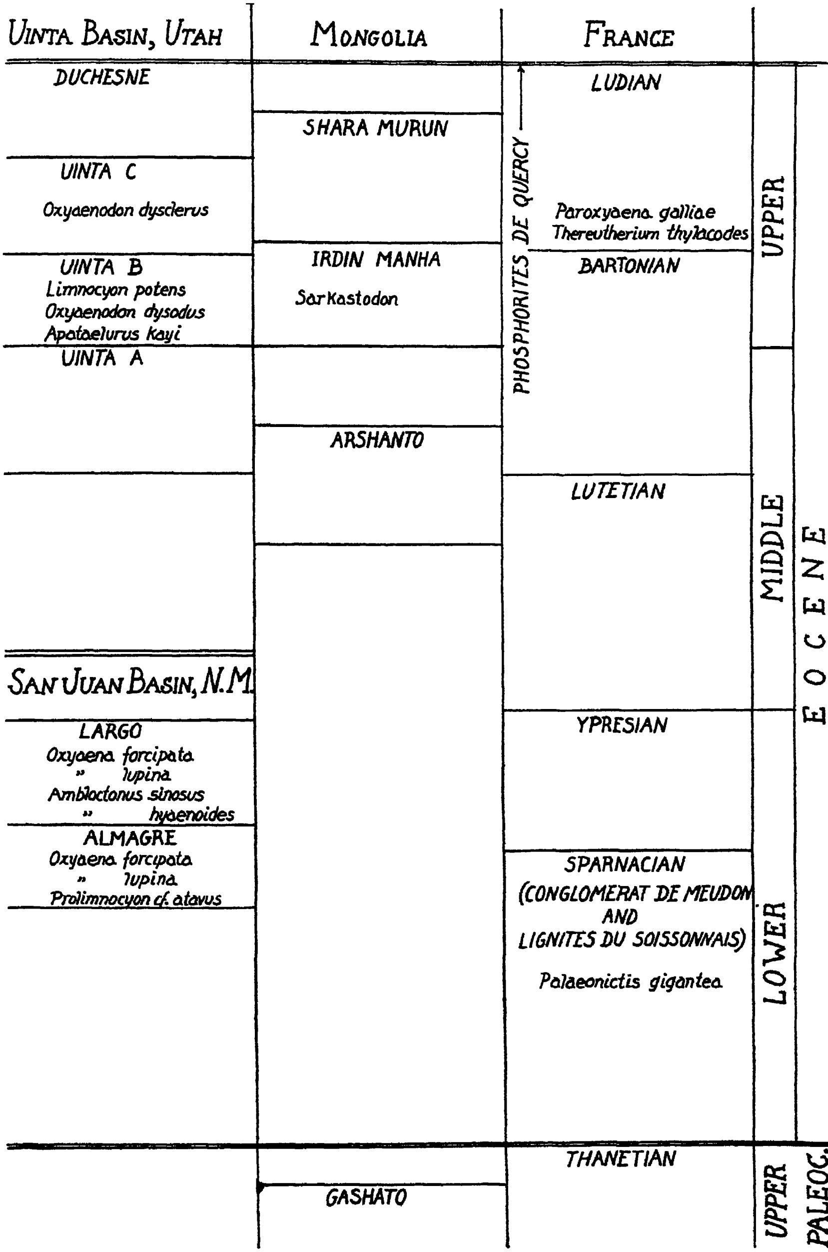


FIGURE 4. Geological and geographical distribution of the broad-skulled Pseudocreodi (Part II).

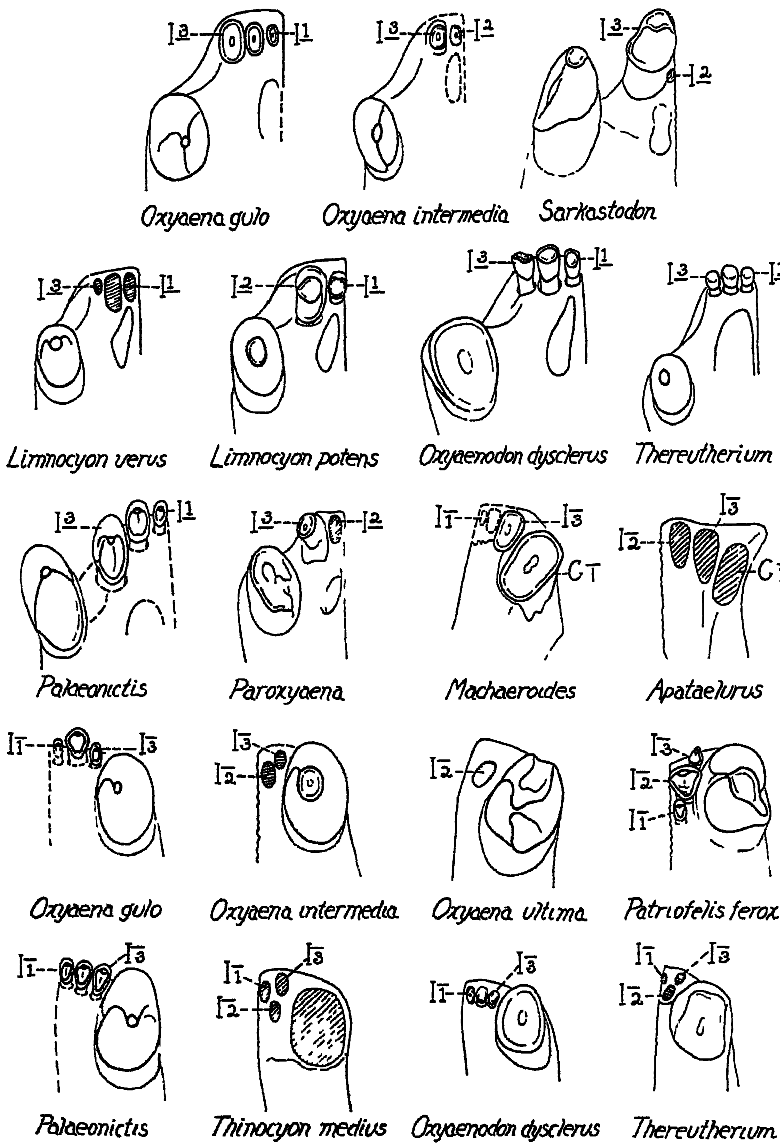


Figure 5. Upper and lower incisors of the broad-skulled Pseudocreodi.

STRUCTURAL AND FUNCTIONAL EVOLUTION

Teeth

INCISORS: (FIGURE 5.) In the ancestral creodonts, the incisors were three in number in each jaw, and, no doubt, small and subequal in size, and arranged in a transverse row. This condition is found in *Oxyaenodon*. The lower incisors of most of the broad-skulled Pseudocreodi, however, are crowded greatly between the canines, and are reduced in size and in number. *Oxyaena gulo* shows the most primitive known state of any of the Oxyaeninae; it still retains three lower incisors arranged transversely, but $I_{\overline{1}}$ and $I_{\overline{3}}$ are reduced. In later members of the subfamily, the incisors exhibit a tendency towards a more antero-posterior arrangement, which is a result of crowding, and both $I_{\overline{1}}$ and $I_{\overline{3}}$ may be lost, as in *Oxyaena ultima*. *Patriofelis* may retain all three incisors (Amer. Mus. No. 12078), but the most anterior ($I_{\overline{3}}$) is lost in another specimen (Yale, Peabody Mus. No. 10940). *Sarkastodon* has only a single lower incisor, probably $I_{\overline{3}}$. This reduction of the lower incisors, and their crowding between the canines can mean only a corresponding diminution of function; where they are used for nipping, as in the Miacidae and most Fissipedia, they are placed anterior to the canine, and are transversely arranged.

The lower incisors of the Palaeonictinae are not well known. *Palaeonictis* is primitive in having three, subequal in size; it is probable, but not certain, that they were arranged transversely. *Ambloctonus sinosus* has one of the incisors somewhat enlarged, and the others reduced; they are crowded, as in the Oxyaeninae.

In the Limnocyoninae, only the thick-jawed *Oxyaenodon* is known to have three subequal incisors, arranged in a transverse row; in this genus it is probably secondary rather than primitive. All the other Limnocyoninae show crowding and displacement of the lower incisors. Instead of assuming an antero-posterior arrangement, as in the Oxyaeninae, the middle incisor moves backwards, and $I_{\overline{1}}$ and $I_{\overline{3}}$ remain at the front of the jaw in *Thinocyon* and *Thereutherium*. There is less functional reduction in this subfamily.

Apataelurus, the sabre-tooth hyaenodontid, has lost $I_{\overline{1}}$, but $I_{\overline{2-3}}$ are large; the much reduced canine is of only slightly greater size. Although their form is not known, all the anterior teeth probably occluded well with the upper incisors and canine, and functioned to nip and tear off flesh. Its ancestor, *Machaeroides*, shows some reduction of the canine and enlargement of $I_{\overline{3}}$; the inner incisors are not known, but there is space enough for a small $I_{\overline{1}}$ as well as $I_{\overline{2}}$.

Since the upper incisors are placed well in front of the canine, they are less crowded, and retain a transverse arrangement. In all the Oxyaenidae, the inner incisors are reduced and I^3 is enlarged. *Oxyaena gulo* and *Palaeonictis* show this condition at an early stage; they retain a small I^1. The type specimen of *Oxyaena intermedia* has lost this tooth, and I^2 is quite small. The Upper Eocene *Paroxyaena* is similar. The third incisor in these forms closes against the antero-internal side of the lower canine, and probably occludes in part with the largest lower incisor (I_3); it would help to hold food, but this arrangement is not adapted for nipping. The latest oxyaenid, *Sarkastodon,* has lost I^1 and has I^2 reduced to a vestige; I^3 is a tremendously large, robust tooth, wearing blunt at the tip. It suggests that the crushing function has extended to the most anterior part of the jaw in this animal.

In the Limnocyoninae, *Oxyaenodon* and *Thereutherium* retain a very primitive arrangement of the upper incisors. In *Limnocyon* I^2 is enlarged and, in contrast to the Oxyaenidae, I^3 is reduced or lost. These teeth wear very blunt, especially in *Limnocyon potens*.

CANINES: (FIGURES 5, 8–15.) In the early Oxyaenidae the canines are of a normal carnivore type, and not especially robust. Both the upper and lower canines have an internal and a posterior vertical ridge. The upper canine differs from the lower in its slighter curvature and also in wear. In the later members of the family the canines become relatively larger and much more robust. This is true of *Patriofelis* and *Sarkastodon* especially. In all the Oxyaenidae, and especially in the later forms, the tips of the canines rapidly wear blunt and become entirely unadapted for piercing flesh; their function was probably limited to holding, and to some extent to crushing food.

The Limnocyoninae have less robust canines in general. They are especially slender and piercing in *Prolimnocyon*. All of the shallow-jawed forms have an abrupt curve in the root of the lower canine as it leaves the jaw. There is also a characteristic sharp, backward curvature in the crown of this tooth in *Limnocyon* and *Thereutherium,* and perhaps in other genera. The upper canine is also more curved than in the Oxyaenidae. *Oxyaenodon* has developed very robust canines.

The Machaeroidinae parallel the true sabre-tooth cats in reducing the lower canine. The reduction is moderate in *Machaeroides*. Although its form is not known in *Apataelurus*, its alveolus shows it to be only slightly larger than the incisors, as in *Hoplophoneus*. In the presence of the very characteristic sabre-tooth modifications, especially the ventral flange on the lower jaw, it is practically certain that the upper canine of *Apataelurus* was an elongate, stabbing tooth such as occurs in *Hoplophoneus* and *Machaerodus*.

LOWER PREMOLARS: (FIGURES 6, 7, 11–15.) In the Oxyaenidae, $P_{\overline{1}}$, when present, is a small, simple, single-rooted and single-cusped tooth. It is absent in *Oxyaena* only as an individual variation, but it is invariably absent in the later Oxyaeninae, *Patriofelis* and *Sarkastodon*. It is not known to be lost in the Palaeonictinae. On the other hand, it is never absent in the Limnocyoninae and Machaeroidinae, and usually has two roots and a heel cusp. This is correlated with the fact that the jaw is never as much shortened or the tooth row as much crowded as in the Oxyaenidae. *Thereutherium*, the latest and most specialized of the Limnocyoninae, and *Thinocyon cledensis* are the only members of the subfamily to have $P_{\overline{1}}$ reduced to a single-rooted, conical tooth. *Machaeroides* has the two roots distinct in the Lower Bridger, partly united in the Upper Bridger, and the Upper Eocene *Apataelurus* has only a very small, single-rooted $P_{\overline{1}}$. This reduction is not due to crowding as in the Oxyaenidae, but is a result of the fact that the function of the cheek teeth is largely restricted to shearing, and is thus located more posteriorly in the jaw.

$P_{\overline{2}-\overline{4}}$ are two-rooted teeth, increasing somewhat in size and complexity posteriorly, but fundamentally similar. $P_{\overline{2}}$ lacks a distinct anterior basal cusp, although there is always an anterior cingulum. On $P_{\overline{3}}$ a separate anterior cusp appears in some *Limnocyon* and *Thinocyon*, and in the advanced Oxyaeninae, *Patriofelis*, *Sarkastodon*, and a few species of *Oxyaena;* the other forms have only a cingulum anteriorly. The anterior cusp is always present on $P_{\overline{4}}$, though it is small in most primitive species. It is strongly developed in the Palaeonictinae, even in the Upper Paleocene *Dipsalodon*. There is a progressive increase in its size in *Oxyaena*, and it reaches its maximum development in *Patriofelis*, but *Sarkastodon* has either reduced it, or evolved from some oxyaenine which had not progressed far in the development of the anterior cusp. It is relatively weak and variable in the Limnocyoninae. In the Machaeroidinae it is elongate and shearing. A heel cusp is always present; on $P_{\overline{2}-\overline{3}}$ it is smaller and crushing; it is longer on $P_{\overline{4}}$, where, with the transition to the molars, its function is more shearing. Anterior and posterior cingula occur on both the external and internal sides. These are strongly developed in the Palaeonictinae, and show a marked tendency to develop small cuspules. The protoconid is always the largest cusp and is crushing in function, except perhaps in the Machaeroidinae, where it is more shearing. The emphasis of the shearing function in the latter group has resulted in the reduction of the anterior premolars ($P_{\overline{1}-\overline{3}}$) which are used ordinarily for crushing.

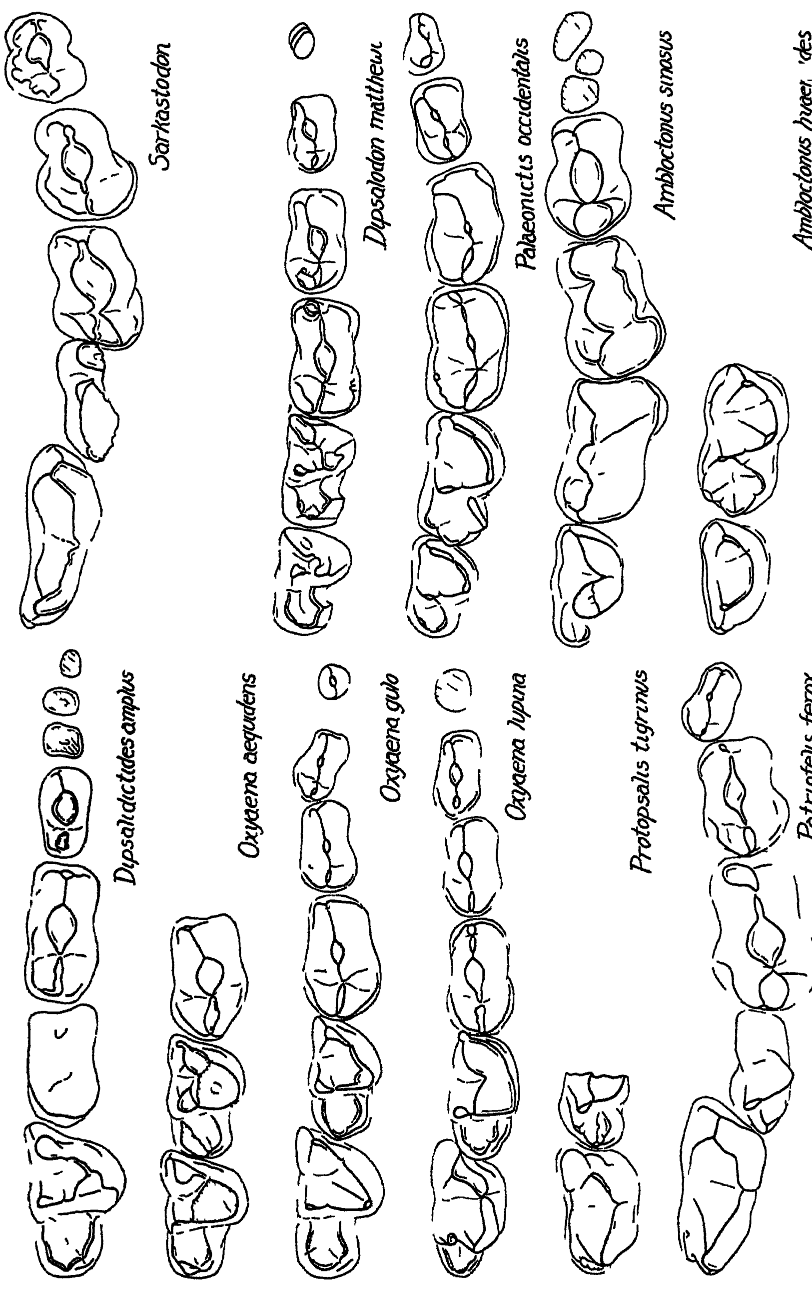


FIGURE 6 Lower cheek teeth of the Oxyaenidae

The proportions of the premolars vary considerably. Among the Oxyaeninae, slender premolars are found in *Dipsalidictides*, *Oxyaena platypus*, *O. lupina* and *O. ultima;* in these the ratio $\frac{\text{width}}{\text{length}}$ of $P_{\overline{1}}$ varies from .51 to 58. Other species, notably *O. aequidens* and *O. forcipata*, have broader premolars with the corresponding ratio of .60 to .63. *Patriofelis* shows a great increase in robustness, and *Sarkastodon* goes

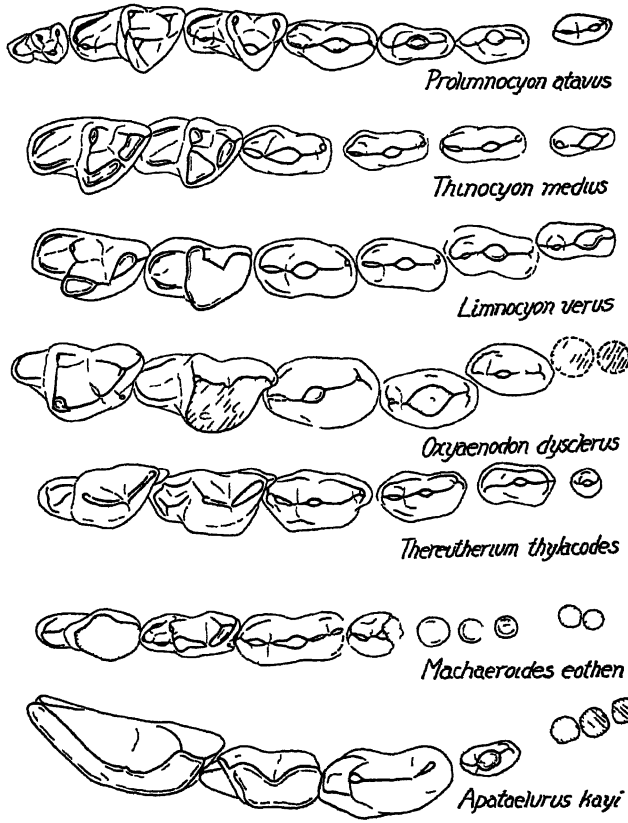


FIGURE 7. Lower cheek teeth of the Limnocyoninae and Machairoidinae.

to extremes in this direction; in the latter genus, $P_{\overline{2}}$ and $P_{\overline{3}}$ are nearly as broad posteriorly as they are long, and may have the posterior root partly divided, an exceptional condition for a carnivore. The Palaeonictinae have rather robust premolars, especially in the later forms. On the other hand, they are generally slender in the Limnocyoninae, although in *Limnocyon potens* and *Oxyaenodon* they become quite robust. In the Machaeroidinae, $P_{\overline{1}}$ is exceptionally long and slender.

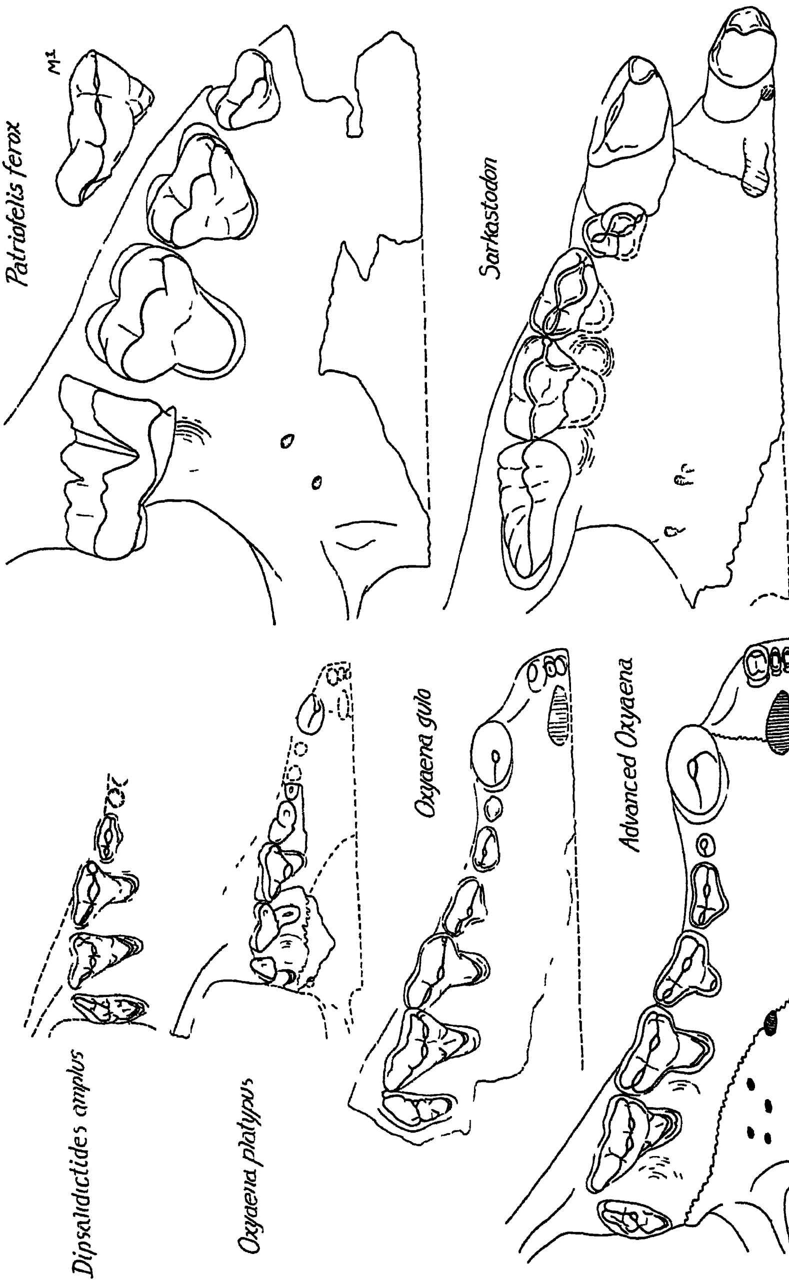


FIGURE 8 Palate and upper teeth of the Oxyaeninae; *Sarkastodon* one third natural size; others three quarters natural size.

UPPER PREMOLARS: (FIGURES 8–10, 14, 15) The first upper premolar agrees closely with the corresponding lower tooth, and the description of the latter is equally applicable here.

$P^{\underline{2}}$ is two-rooted, except in *Patriofelis* and *Sarkastodon*. It never develops a distinct anterior cusp, but there is always an anterior cingulum. A postero-external cusp is present, but is quite small in the early species of *Oxyaena*. In the Limnocyoninae there is no indication of a protocone or internal cusp, but in *Palaeonictis* and the Oxyaeninae there appears a postero-internal swelling, which becomes quite marked in some specimens of *Oxyaena forcipata*, and develops into a distinct protocone in *Patriofelis* and *Sarkastodon*. Accompanying this change, the posterior root expands transversely, and in the last named genera a third or inner root has separated.

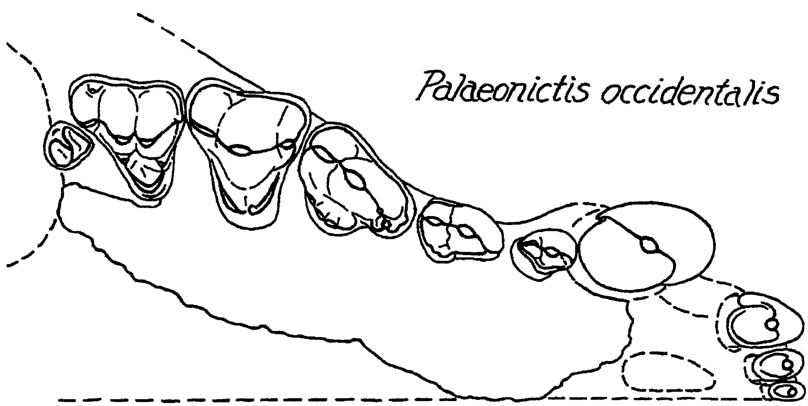


FIGURE 9. Palate and upper teeth of Palaeonictinae, nine eighths natural size.

In the Oxyaeninae, the primitive $P^{\underline{3}}$ is similar to $P^{\underline{2}}$, two-rooted, and without a trace of a protocone lobe; this condition is exemplified by *Dipsalidictides* and *Oxyaena platypus*. In intermediate species of *Oxyaena*, such as *O. transiens*, *O. gulo* and *O. intermedia*, the inner root has separated or is separating, and there is a small internal lobe, which does not bear, however, a distinct protocone. In *O. lupina* and *O. forcipata* this protocone lobe is large and has a distinct cusp. *Patriofelis* and *Sarkastodon* are advanced further in the large size of the protocone. In the Palaeonictinae, *Palaeonictis* has an inner lobe bearing variable small cuspules, one or several of which may be homologous with the protocone. The Limnocyoninae differ markedly in that the most primitive genus, *Prolimnocyon*, has a three-rooted $P^{\underline{3}}$,

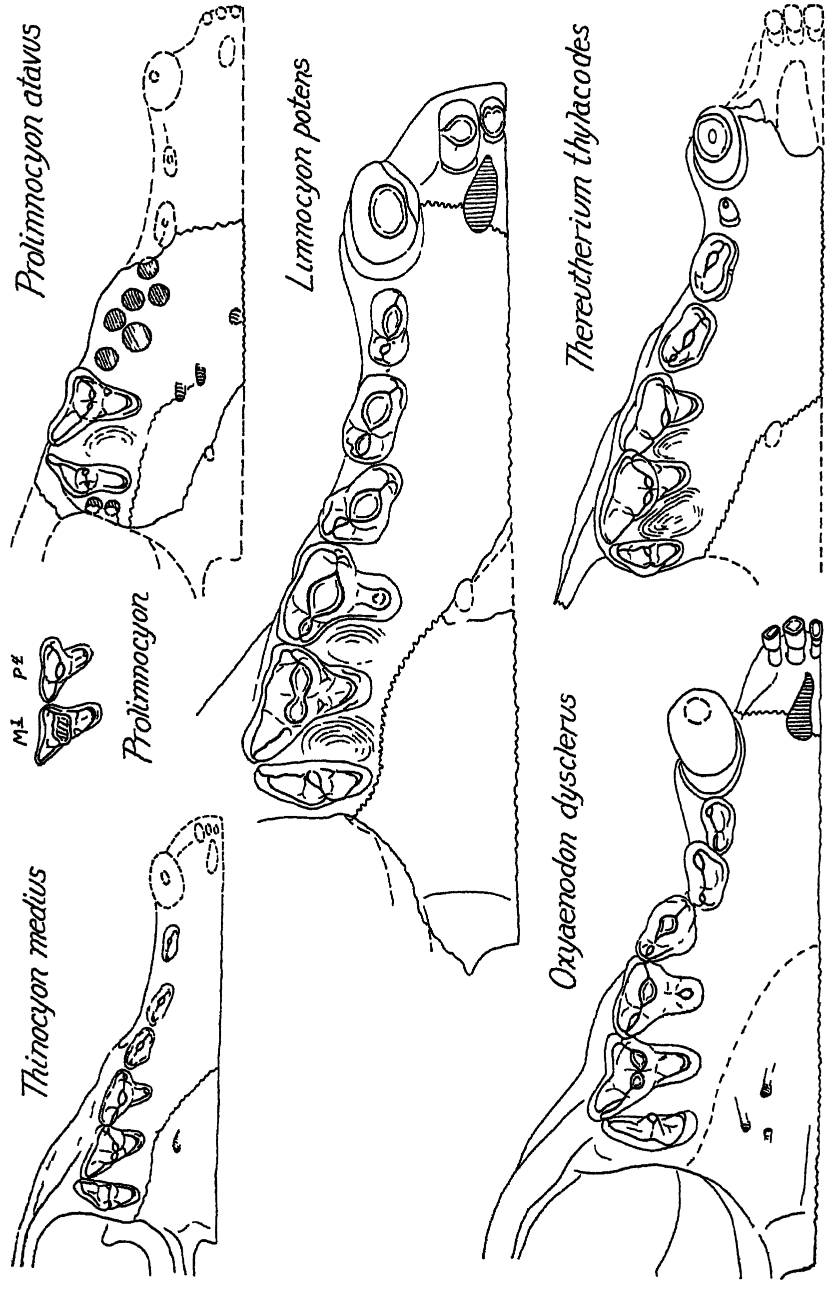


FIGURE 10. Palate and upper teeth of the Limnocyoninae; *Thereutherium* three times natural size; others, four thirds, natural size

while most of the later genera have this tooth simple and two-rooted, never with a distinct protocone. In the nearly related Proviverrinae, *Sinopa* lacks the internal root but may have an internal swelling, which is lacking in advanced species and genera of this group. This suggests a simplification, which is apparently what has taken place in the Limnocyoninae. Moreover, an investigation of the early Paleocene Creodonta reveals that the protocone is almost always present on $P^{\underline{3}}$, thus its presence is a primitive character, and it was probably present in the ancestors of the Proviverrinae and Limnocyoninae. On the other hand, there is every indication that the immediate ancestors of the Oxyaeninae did not possess a protocone; this may mean that they had never developed it, or possibly that they had lost it early. The presence of the internal root on $P^{\underline{3}}$ of *Oxyaenodon* may be a retention of a primitive character, but the evidence is inconclusive.

$P^{\underline{4}}$ always has a large internal root and a well developed protocone. In all the Limnocyoninae except *Thereutherium* the protocone is a simple conical cusp, but in the Oxyaeninae the protocone develops anterior and posterior ridges or cingula which increase in size and, in advanced *Oxyaena* and *Patriofelis*, give a more basined character to the inner lobe of $P^{\underline{4}}$. This basin forms a more efficient crushing apparatus than the simple, conical protocone, and its posterior edge extends the surface against which the paraconid of $M_{\overline{1}}$ shears. *Thereutherium* approaches the oxyaenine type in this respect. *Palaeonictis* has the anterior and posterior cingula well developed. $P^{\underline{4}}$ differs also from $P^{\underline{2-3}}$ in the presence of an anterior cusp or parastyle. The postero-external cusp, or metastyle, is usually elongate, and forms the external part of the shearing surface for the paraconid and protoconid of $M_{\overline{1}}$. It is shortest in *Palaeonictis*, in which the shearing function is least emphasized.

LOWER MOLARS: (FIGURES 6–7, 11–15.) Among the broad-skulled Pseudocreodi, $M_{\overline{3}}$ is retained only in *Prolimnocyon*, where it is much reduced or vestigial. It is largest in *P. robustus*, in which all of the essential elements are present. In *P. atavus* it is much smaller and variable; the two roots may be separate or united; only a single talonid cusp remains, and the metaconid may be lost. In *P. antiquus* it is very small and single-rooted. This genus emphasizes the close relationship of the Limnocyoninae and Proviverrinae. In the contemporary *Sinopa*, a member of the latter subfamily, $M_{\overline{3}}$ is usually the largest of the lower molars, but in *S. mordax*, and to a lesser degree in *S. sternua*, $M_{\overline{3}}$ is reduced.

In all the most primitive members of this group, $M_{\overline{1}}$ and $M_{\overline{2}}$ are

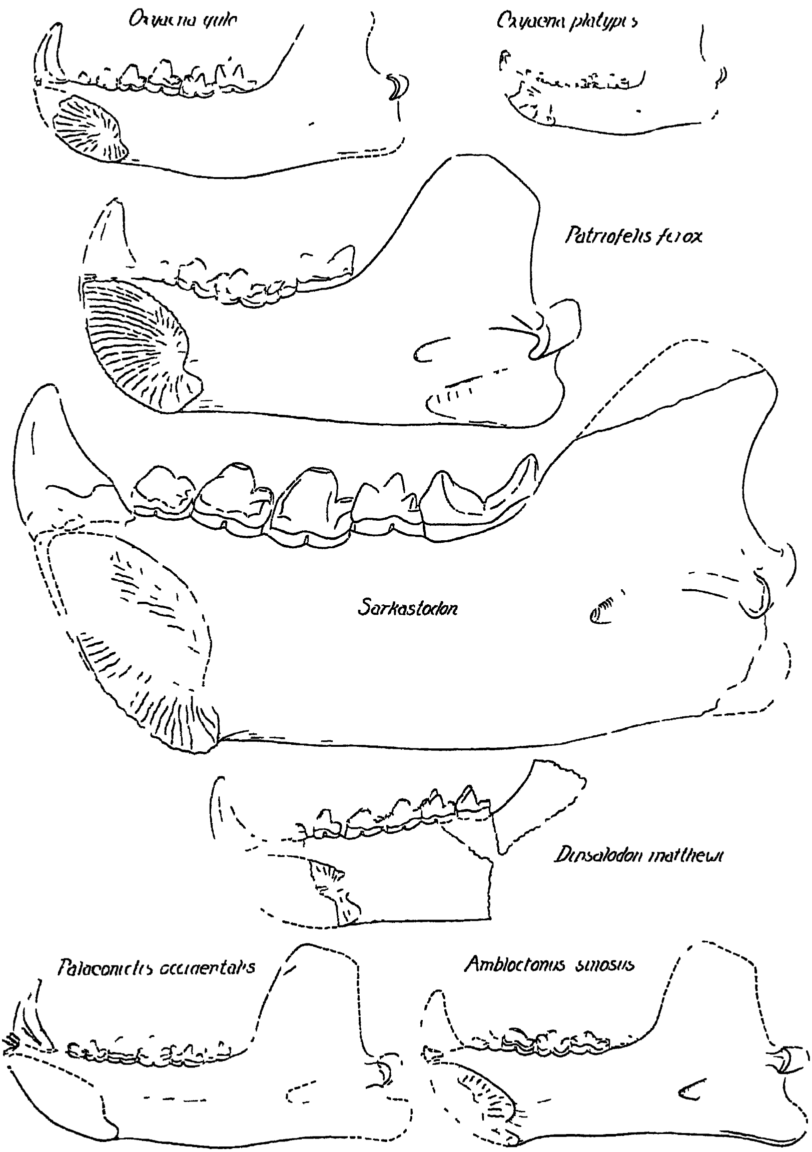


Figure 11. Internal view of lower jaw of the Oxyaenidae; one third natural size.

similar and subequal, tuberculo-sectorial, with the paraconid only slightly larger than the metaconid, and with the talonid unreduced.

In the Oxyaeninae, starting from this point, $M_{\overline{2}}$ is enlarged and $M_{\overline{1}}$ reduced, and the paraconid-protoconid shearing blades of both teeth are enlarged, especially that of $M_{\overline{2}}$. Thus the latter tooth is designated as the carnassial. The transformation of a tuberculo-sectorial $M_{\overline{2}}$ into a sectorial tooth involves the reduction and loss of the metaconid and talonid, the elongation of the paraconid and protoconid, and the rotation of the shearing surface until it parallels the axis of the jaw. This evolution is expressed numerically for $M_{\overline{2}}$ in TABLE 1.

Species	Length $\frac{M_{\overline{1}}}{M_{\overline{2}}}$	Tri[d] $\frac{W}{L}$	$\frac{\text{L. tal}^d}{\text{L. tooth}}$	Shear angle
Oxyaena platypus	1.00	1.09	.42	60°
O. aequidens	.98	1.05	.39	60°
O. transiens	.89	1.02	.35	50°
O. intermedia	.90–.91	.91–.97	.36–.39	40°–45°
O. gulo	.84	.91–.97	.33–.37	40°–45°
O. forcipata	.77–.86	.77–.85	.28–.34	30°–35°
O. lupina	.86–.87	.75–.79	.28–.33	30°–35°
Protopsalis tigrinus	—	.57	.16	very low
Patriofelis compressa	.82	.41	0	0°
P. ferox	.81	.48	.02	0°

TABLE 1. Numerical expression of the evolution of $M_{\overline{2}}$ in the Oxyaenidae.

The talonid of $M_{\overline{2}}$ differs from that of $M_{\overline{1}}$ in having the cusps less distinct, and usually forming a nearly continuous ridge. In *Patriofelis* and *Sarkastodon* the talonid is minute, or represented only by a short cingulum.

Although $M_{\overline{1}}$ undergoes the same changes as $M_{\overline{2}}$, it lags far behind the latter tooth, and never becomes a true sectorial. In *Oxyaena* and *Protopsalis* the hypoconid, hypoconulid and entoconid are moderately distinct, and the heel is basined; but in *Patriofelis* the talonid becomes shearing by the reduction of the entoconid and the development of the hypoconid into a median, antero-posterior ridge. The trigonid of $M_{\overline{1}}$, especially the paraconid and protoconid, become elongate and more shearing in the later Oxyaeninae, but a small metaconid is always retained.

The lower molars of the earliest of the Palaeonictinae, *Dipsalodon*, are very close to those of primitive species of *Oxyaena*, but $M_{\overline{2}}$ is very slightly smaller than $M_{\overline{1}}$ ($M_{\overline{1}}/M_{\overline{2}}$ 1.05). This genus helps to connect the two subfamilies in tooth structure. In *Palaeonictis* the reduction of $M_{\overline{2}}$ has gone much further ($M_{\overline{1}}/M_{\overline{2}}$ 1.15–1.43).

Both molars are essentially tuberculo-sectorial. . The paraconid-protoconid shear is slightly enlarged and has a characteristic outward convexity; the metaconid is only slightly reduced on M_1, but is variable on M_2 where it may be vestigial. A characteristic feature of the Palaeonictinae is the distinctness and large size of the talonid cusps of M_1; on M_2 only the hypoconid and entoconid are present, and they may be quite indistinct. In *Ambloctonus*, M_1 is essentially similar except that its trigonid has a more crescentic form. M_2 is more specialized in that the metaconid is completely absent, and the talonid is much reduced or vestigial. The paraconid and protoconid form a shearing blade which is strongly convex outward. Although much smaller and less efficient as a sectorial than the corersponding tooth of the Oxyaeninae, it is nevertheless *the* carnassial.

M_{1-2} of the Limnocyoninae are much less progressive than those of the Oxyaenidae. In *Prolimnocyon* they are of a primitive tuberculo-sectorial type, with unreduced metaconids and relatively long talonids. *Limnocyon* and *Thinocyon* are advanced only in the simplification of the talonids and slight elongation of the paraconid-protoconid shears and reduction of the metaconids. The Upper Eocene *Oxyaenodon* carries these tendencies a bit farther, and has the talonid of M_2 somewhat reduced. *Thereutherium* is the most specialized member of the group; it has lost the metaconid completely, and has a well developed paraconid-protoconid shear, nearly paralleling the jaw axis, but the talonids are reduced very little. An important difference between the Limnocyoninae and Oxyaenidae is that M_1 is reduced only slightly in the former.

In the Machaeroidinae, the sectorial specialization is much more extreme than in any of the Limnocyoninae. The lower molars of *Apataelurus* parallel those of *Patriofelis* so closely that a near relationship is strongly suggested. But *Machaeroides*, an undoubted offshoot of the Limnocyoninae, shows many advances in the direction of *Apataelurus* and serves to connect the latter genus with the Limnocyoninae. *Machaeroides* has very slender, sectorial molars in which the talonids are still large; but the metaconid is much reduced on M_1 and may be absent on M_2.

UPPER MOLARS: (FIGURES 8–10, 14, 15.) A small M^3 is present in *Prolimnocyon atavus*, indicated by two alveoli in Amer. Mus. No. 15171. In the other broad-skulled Pseudocreodi, M^3 is absent.

In all the members of this group, M^2 is transversely placed, vestigial or absent. This condition contrasts with the long-faced Pseudocreodi, Proviverrinae and Hyaenodontinae, in which M^2 is the main upper

carnassial. In the intermediate form, *Prolimnocyon*, it is least reduced; its postero-external corner is moderately prominent and the metacone is distinct. In later Limnocyoninae the metacone is vestigial or absent, but M^2 is always present since it occludes with the talonid of M_2 which is relatively unreduced in this subfamily. In the Oxyaeninae, M^2 is present in *Oxyaena* which retains a talonid on M_2, and absent in *Patriofelis* and *Sarkastodon* in which the talonid is lost. When present, the metacone is indistinct. In both the Limnocyoninae and Oxyaeninae M^2 has three roots, one external, one internal and a small posterior one. In *Palaeonictis* M^2 is variable. In Amer. Mus. No. 16960 it has three roots; in No. 16116 it is a very slender, transverse, two-rooted tooth, lacking a metacone; in No. 110 it is a small, round, single-rooted vestige. A small M^2 is present apparently in *Ambloctonus sinosus*, but it may be lacking in *A. hyaenoides* which has nearly lost the talonid of M_2.

The primitive M^1 of the Limnocyoninae and Oxyaeninae has the paracone and metacone partly connate, a moderately long metastyle and a short parastyle, large protocone, and small protoconule and metaconule. In the earliest oxyaenine, *Dipsalidictides*, M^1 is much wider transversely than long due to the exceptionally well developed protocone and small metastyle. It is possible but not certain that this is the primitive condition for the group. In the other Oxyaeninae the metastyle is progressively elongate and the protocone reduced. This brings about a lengthening of the shearing surface and a rotation of this surface until it becomes nearly parallel to the cheek tooth-row, thus forming a more effective sectorial. The culmination of this evolution is found in *Patriofelis* and *Sarkastodon*, in which the protocone is vestigial and the shearing blade is very long and made up half by the metastyle and half by the conjoined paracone and metacone. In the Limnocyoninae, the metastyle is never as much elongate nor the protocone as much reduced, and M^1 retains a distinctly tritubercular appearance. The first molar of the Palaeonictinae has quite a different appearance, largely due to the fact that the metastyle is quite short and the paracone and metacone are less closely conjoined. But as Matthew pointed out (1909, p. 411), this tooth is the carnassial, although its sectorial function is not emphasized as much as in the Oxyaeninae. Its antero-external angle is very short, not lengthened as in those forms which have a carnassial P^4.

MILK DENTITION: The tooth succession of the broad-skulled Pseudocreodi agrees well with that of the fissipedes. Both upper and lower milk teeth of *Oxyaena* are well known from several individuals.

The lower milk molars of *Patriofelis* were considered to be a distinct genus, *Aelurotherium*, until Matthew showed their correct affinity (1909, p. 419); his conclusions are confirmed by a specimen in the U. S. National Museum (No. 13318) bearing $DP_{\overline{2}-\overline{1}}$ and $M_{\overline{1}}$ erupting. Some of the milk dentition is known in *Palaeonictis* and *Ambloctonus*, and it is thoroughly described in *Thereutherium* by Martin (1906, p. 592). As is usually the case, each milk tooth agrees closely with the permanent tooth just behind the one which succeeds it; for example, $DP^{\underline{4}}$ resembles $M^{\underline{1}}$. The milk teeth are usually smaller and of more slender proportions. The tooth between $DP_{\overline{2}}$ and $DC_{\overline{1}}$ is probably $P_{\overline{1}}$; in any case, there is no evidence that it has a successor.

Lower Jaw

The lower jaw (FIGURES 11–15) is usually one of the most numerous and best preserved of fossil remains and as such is more susceptible to exact measurement and proportional study. Four ratios are found to be especially significant: (1) Depth ratio; inside depth of lower jaw at anterior root of $M_{\overline{2}}$ divided by length of jaw, condyle to chin. (2) Dental ratio; length of lower cheek tooth row divided by length of jaw. (3) Condyle ratio; transverse width of condyle divided by length of jaw. (4) Thickness ratio; thickness of jaw at M_2 divided by depth of jaw at $M_{\overline{2}}$.

Species	Depth ratio	Dental ratio	Condyle ratio	Thickness ratio
Oxyaena platypus	208	175	19	38
O. gulo	.237	170		37
Patriofelis coloradensis	261	118	25	30
P. ferox	.245	390	28	40
Sarkastodon	.271	527	--	--
Palaeonictis occidentalis	.237	419	19	34
Ambloctonus sinosus	.241	428	26	.36
Prolimnocyon atavus	.176	500	--	52
Thinocyon velox	.135	548	14	57
T. medius	163	508	15	50
Limnocyon verus	210	451	19	17
Oxyaenodon dysclerus	187	469	19	58
Thereutherium thylacodes	.155	520	16	64
Apataelurus kayi	.171	403	20	49

TABLE 2. **Jaw ratios of the broad-skulled Pseudocreodi.**

In TABLE 2 it is shown that the jaw is relatively deep in the Oxyaeninae and Palaeonictinae, and becomes relatively deeper in advanced

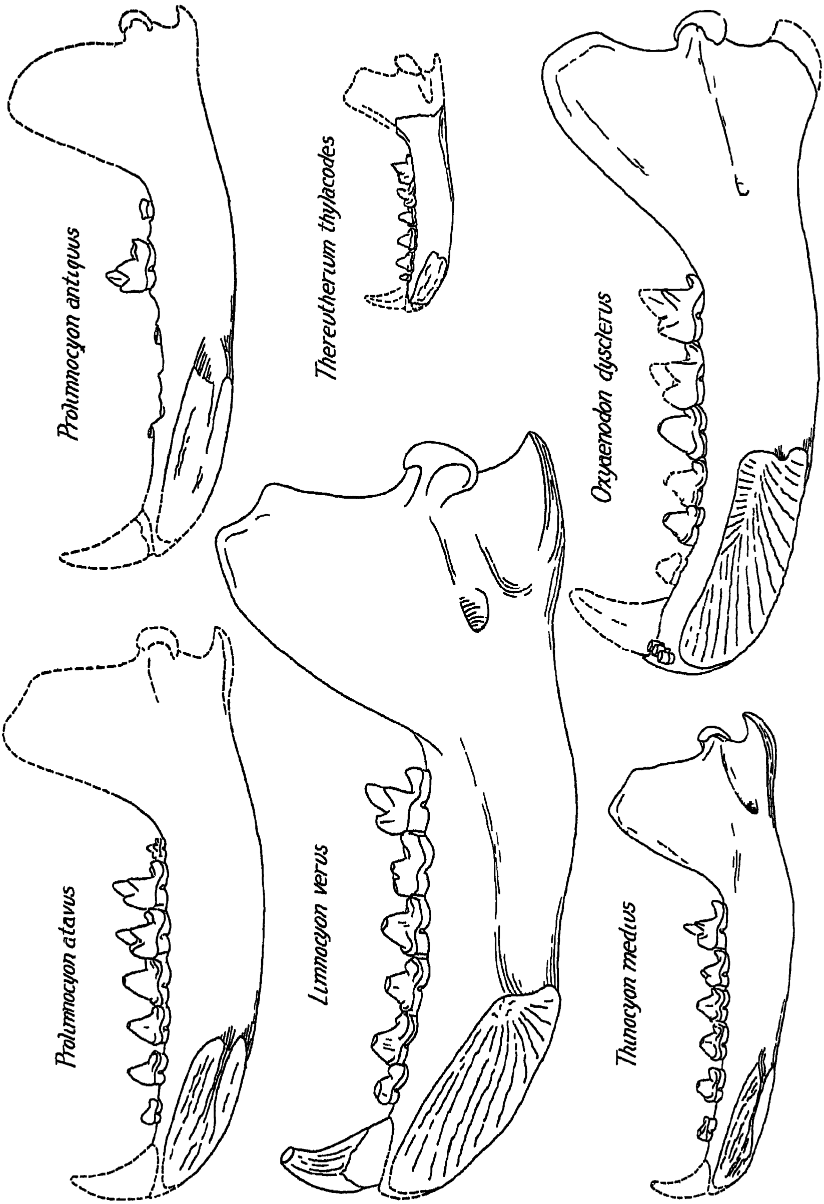


FIGURE 12 Internal view of lower jaw of the Limnocyoninae. natural size.

forms. Because of the great depth, the jaw is relatively thinner than in the Limnocyoninae, but it is still quite robust in most forms. The cheek tooth-row is short in the Oxyaenidae. The depth and dental

ratios are dependent on and correlated with the shortening of the jaw as a whole. This is extreme in *Patriofelis*, *Sarkastodon* and *Ambloctonus*. The jaw of the Limnocyoninae is relatively long, shallow and thick, with a moderate to long tooth row. Only *Limnocyon* approaches the Oxyaenidae in jaw proportions, while *Prolimnocyon*, *Thinocyon* and *Thereutherium* are at the other extreme. *Oxyaenodon* has a peculiarly thick, robust jaw. The Machaeroidinae differ in having a relatively long jaw but short tooth-row. For its moderate depth, the jaw is thin.

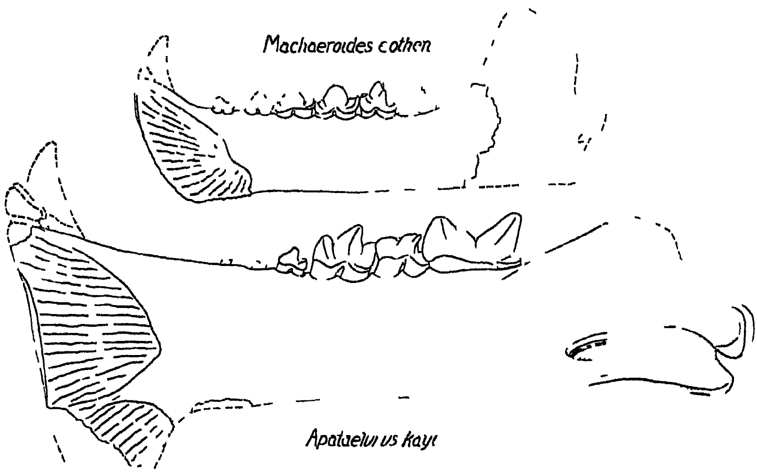


FIGURE 13 Internal view of lower jaw of the Machaeroidinae, two thirds natural size

The robust symphysis is spoken of often as being characteristic of the Oxyaenidae, although it also occurs in the Mesonychidae and Triisodontinae. The Limnocyoninae are transitional to the more typical Hyaenodontidae in this respect. In the shallow-jawed forms, *Prolimnocyon*, *Thinocyon* and *Thereutherium*, the symphysis is long, shallow and inclined only slightly, and the front of the jaw slopes up very gradually; it does not differ very strongly from the symphysis of certain species of *Sinopa*. In *Limnocyon* the symphysis is deeper and more steeply inclined. In *Oxyaenodon* it is fairly strong, but horizontally placed, and follows the peculiar abrupt curvature of the jaw anteriorly. The Machaeroidinae have a different specialization; this involves steepening of the anterior face of the jaw until it is almost vertical, and deepening of the symphysis. In *Apataelurus* the symphysis is extended onto the ventral flange which protects the upper canine.

In the earliest and most primitive Oxyaenidae, *Oxyaena platypus* and *Dipsalodon*, the symphysis is stronger than in the heaviest-jawed

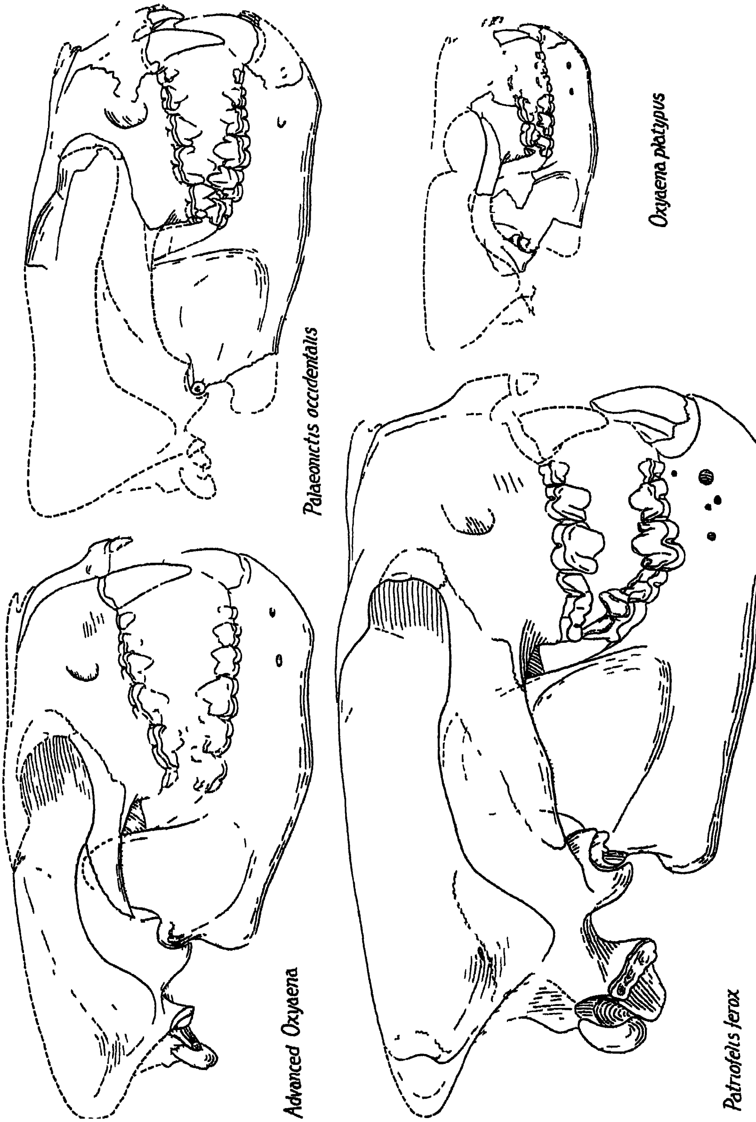


FIGURE 14. Lateral view of the skull and jaw of the Oxyaenidae, one third natural size.

Limnocyonine. Moreover, it increases in relative size and in inclination in later forms until, in *Patriofelis* and *Sarkastodon*, it forms a

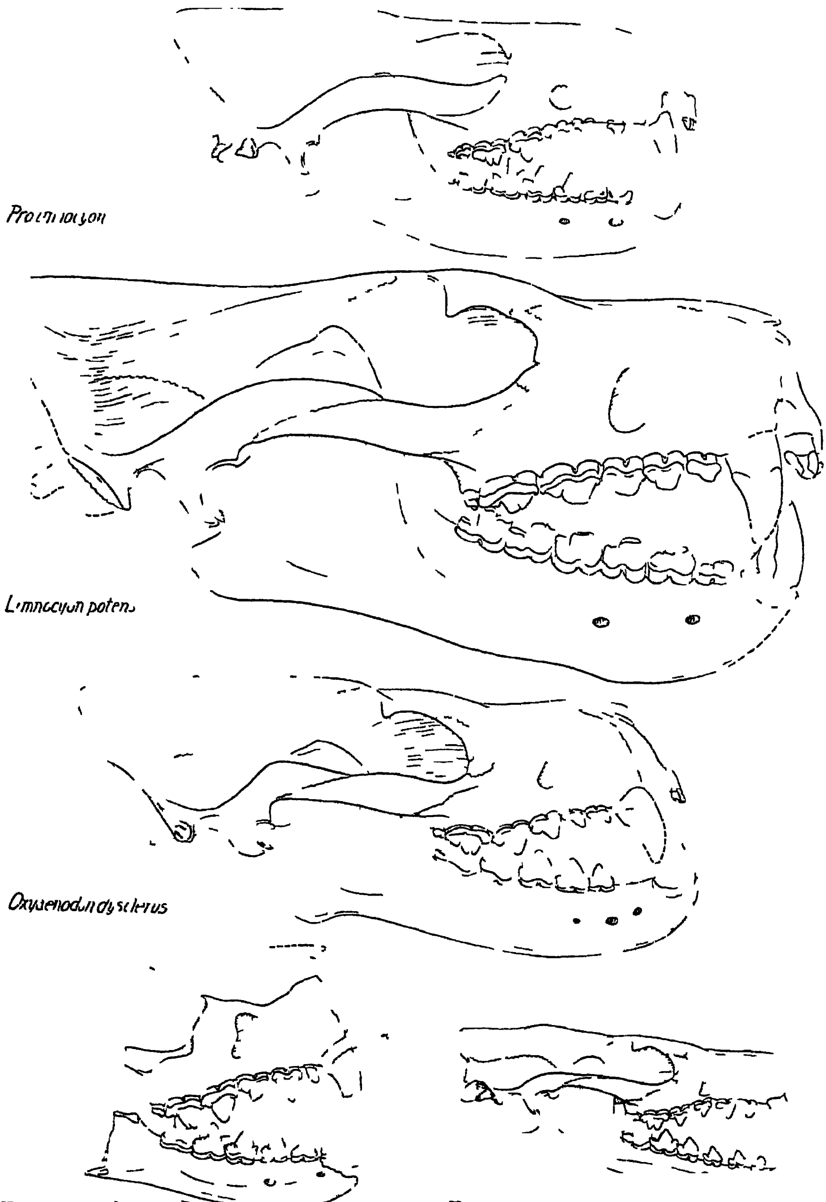


FIGURE 15 Lateral view of the skull and jaw of the Limnocyoninae; *Thereutherium* four thirds natural size, others two thirds natural size

tremendously solid jaw attachment. Accompanying this change, the anterior face of the jaw becomes much steeper.

Ordinarily there are two mental foramina on the outer side of the jaw, an anterior placed under $P_{\overline{1}}$ or $P_{\overline{2}}$, and a posterior under $P_{\overline{3}}$ or $P_{\overline{4}}$. In *Patriofelis* they are commonly subdivided into a number of small foramina. Extra foramina occasionally occur in other forms. The position of the foramina is variable and is of little systematic importance, except in the Machaeroidinae in which both foramina are placed very low in the jaw.

The above table shows that the condyle is narrow in the long, shallow, weak-jawed Limnocyoninae, and is much wider in the more robust-jawed Oxyaenidae, especially in *Patriofelis, Sarkastodon* and *Ambloctonus*. The wide condyle furnishes a stronger hinge. In correlation with the presence of a preglenoid crest in the Oxyaenidae, the articular surface of the condyle extends dorsally onto the anterior surface; it is less extensive in the Hyaenodontidae where the preglenoid crest is absent. The condyle is usually placed at about the height of the cheek tooth-row, as in the case of carnivores generally. This facilitates shearing by allowing the posterior carnassial teeth to come into action first. In the Machaeroidinae the condyle is exceptionally low, as in the true sabre-tooth cats; this makes possible a much wider gape.

The angular process is of considerable systematic importance. In the Oxyaeninae it is very short, projects only slightly, and is deep and bluntly rounded. In the Palaeonictinae it projects behind the condyle, but is bluntly rounded as in the Oxyaeninae. In the Limnocyoninae, the angle is long, slender, and slightly upcurved and pointed at the tip; there is an inner shelf below the insertion area of the pterygoid muscles which gives it a slightly inflected appearance, especially in *Thinocyon*. *Apataelurus* has reduced and blunted the angle to allow a wider gape.

The coronoid process is strongly developed in all the broad-skulled Pseudocreodi except the Machaeroidinae. In *Apataelurus* it is extremely low, as in the true sabre-tooth cats. As Matthew has demonstrated (1910, p. 298 and 303), this allows the lower jaw to be opened much wider because of the greater length of the temporal muscle and its correspondingly great stretching range.

Another peculiar character of the Machaeroidinae is the lateral flare at the anterior end of the jaw, and the flat anterior face of the jaw. The increased width anteriorly enables the much reduced lower canine to move forward and to become functionally part of the incisor series.

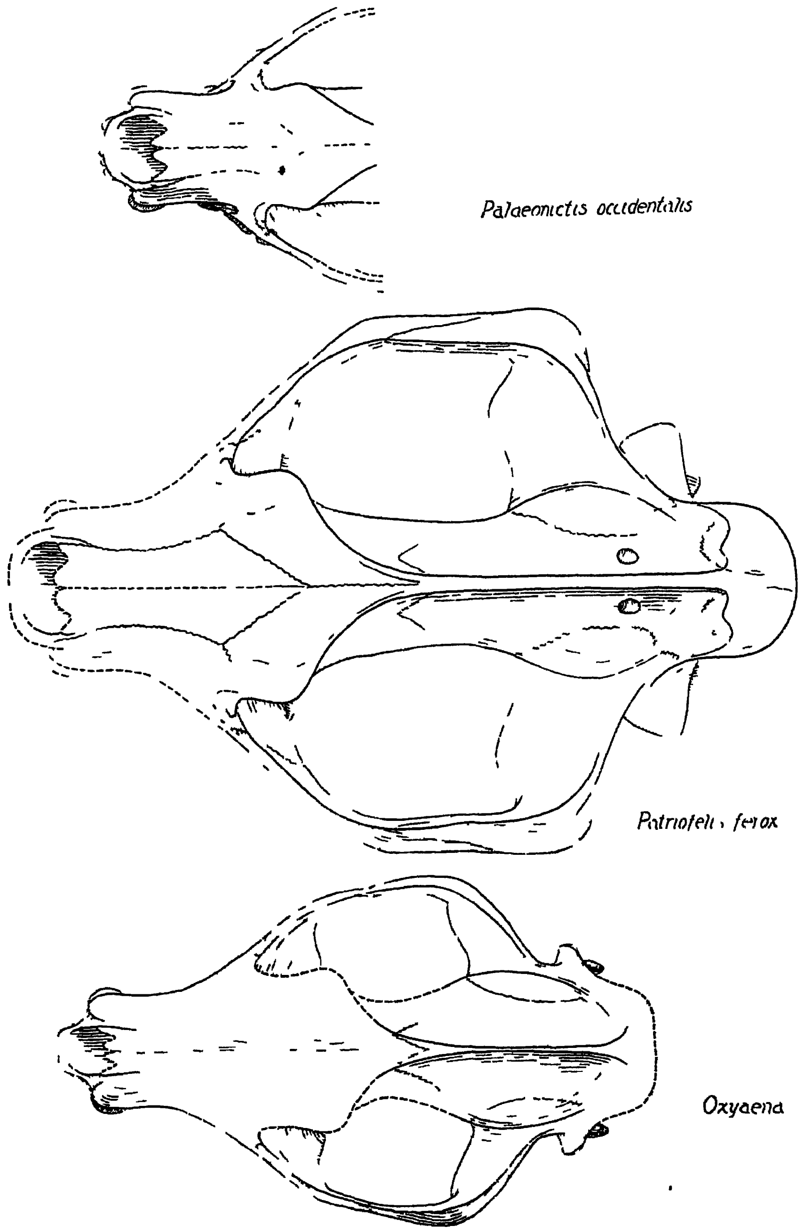


FIGURE 16 Dorsal view of skull of the Oxyaenidae, one third natural size.

Skull

PROPORTIONS: It is not possible to make as exact a proportional analysis of the skull as of the lower jaw because the material is less abundant and usually crushed or fragmentary. The few measurements given are from the better preserved skulls and from the carefully made restorations. Although they give a general idea of the skull proportions, they cannot be relied upon to be absolutely correct. The following measurements are taken as in Osborn, 1912 (pp. 85–86): basilar length, from median incisive border to anterior edge of foramen magnum; frontal width, or width at posterior border of orbits; facial length, from median incisive border to middle of line connecting posterior borders of orbits; length of upper molar-premolar series; also taken was the greatest width of the skull which is at the posterior part of the zygomatic arch. The following ratios are significant: *cephalic index* (frontal width × 100 ÷ basilar length); *facio-cephalic index* (facial length × 100 ÷ basilar length); *dental index* (length of upper molar-premolar series × 100 ÷ basilar length); and, *zygomatic index* (greatest width × 100 ÷ basilar length).

Species	Cephalic index	Facio-cephalic index	Dental index	Zygomatic index
Sinopa grangeri	43	51	41	52
Thinocyon velox	51	51	36	58
Limnocyon verus	49	47	35	61
L. potens	50	48	34	61
Oxyaenodon dysclerus	60	54	35	70
Oxyaena (restoration)	58	49	35	66
Patriofelis ferox	63	42	28	80

TABLE 3 Indexes showing general skull proportions

The cephalic and zygomatic indexes show the relative breadth or brachycephaly. *Sarkastodon*, for which figures are not obtainable, and *Patriofelis* have excessively broad skulls with widely expanded zygomatic arches, while their ancestor, *Oxyaena*, is less brachycephalic, but still more so than most of the Limnocyoninae. *Palaeonictis* probably has a skull as broad or broader than that of *Oxyaena*. *Oxyaenodon*, one of the latest and most specialized of the Limnocyoninae, is comparable to the Oxyaeninae in its brachycephaly, but the other members of the subfamily are intermediate to the narrow-skulled *Sinopa* in skull proportions. *Prolimnocyon* is undoubtedly the least brachycephalic of the group.

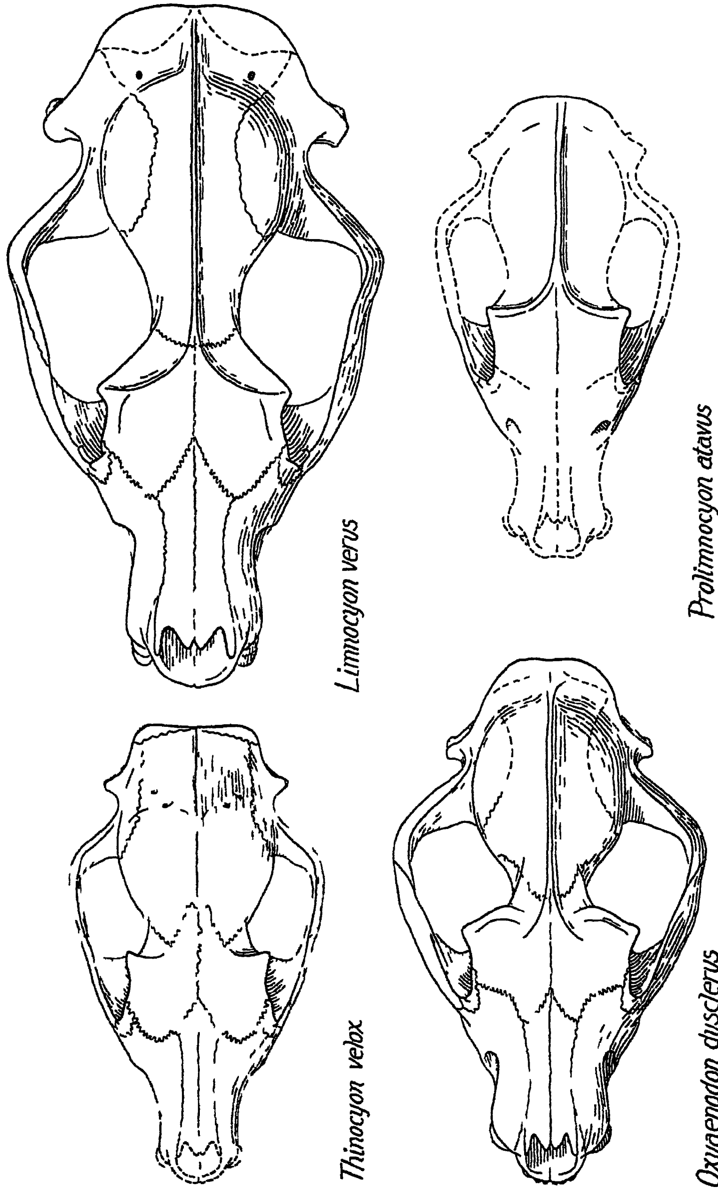


FIGURE 17 Dorsal view of skull of the Limnocyoninae *Thinocyon* nine tenths natural size, others three fifths natural size

The facio-cephalic index is a measure of the relative length of the facial region. All of the Limnocyoninae, even the broad-skulled

Oxyaenodon, have a moderately long facial region as in other Hyaenodontidae. In early Oxyaeninae the face is also moderately long, but it is greatly shortened in *Patriofelis* and *Sarkastodon*. In the Lower Eocene *Palaeonictis* the facial region is precociously short.

The shortening of the upper cheek tooth-row is closely correlated with the shortening of the face. In *Prolimnocyon*, which retains M^3, the relative length of the tooth-row is comparable to that of *Sinopa*. The other Limnocyoninae and *Oxyaena* have the tooth-row shortened by the loss of M^3, while *Patriofelis* and *Sarkastodon*, lacking both M^{2-3} and P^1 have an extremely reduced cheek tooth-row.

FACIAL REGION: (FIGURES 14–17.) In the Limnocyoninae the maxillary bones are long and shallow and the nasals are relatively narrow. In the short-, broad-faced Oxyaenidae the maxillaries are deepened and shortened, and the nasals are shortened and widened. The nasals are wide anteriorly, constricted at the middle of their length, and wide again at the maxillo-frontal suture; from here they taper to a pointed posterior termination, which is well in front of the postorbital process in most Limnocyoninae, and opposite or behind this process in *Limnocyon potens* and the Oxyaenidae. The form of the nasals is similar in the Marsupialia, Hyaenodontidae, Mesonychidae and many of the Arctocyonidae; it is widely different from the unconstricted, bluntly terminated nasals of *Deltatherium* and the Miacidae. The anterior ends of the nasals are notched in the Limnocyoninae; the extremely broad nasals of *Sarkastodon* terminate bluntly anteriorly. The anterior opening of the infraorbital canal in the maxillary is over P^3, a constant feature in the Carnivora. As in all primitive mammals, the lachrymal has a rather large facial extent; this is probably somewhat reduced in *Palaeonictis*.

PALATAL REGION: (FIGURES 8–10.) The palate of *Oxyaenodon* and the later Oxyaenidae is shortened and broadened along with the face. In *Sarkastodon* and *Patriofelis* it is too short to include all of the much reduced cheek tooth-row, for the posterior part of M^1 extends onto the zygomatic arch. The relative length of the palate in *Prolimnocyon*, as estimated from the length of the lower jaw, is greater than in other members of this group, and approaches *Sinopa* in this, as in other respects. The earlier Oxyaenidae and the other Limnocyoninae are intermediate in proportions. The palate is pierced anteriorly by the anterior palatal foramina, and posteriorly in the palatine bone by a variable number of small posterior palatal foramina, as in all Carnivora. Along the median line, the posterior termination of the palate is variable in position, in front of M^2 in *Oxyaena*, behind

M^1 in *Patriofelis* and *Sarkastodon*, slightly behind M^2 in *Thinocyon*, while in *Limnocyon potens* and *Oxyaenodon* it is far behind the posterior end of the cheek tooth-row. The posterior extension of the hard palate, as in the latter two forms, is not unusual among Carnivora, but its functional significance, if any, is not known. At or near the posterior end of the palate is a swollen ridge such as occurs also in the Hyaenodontidae and many Arctocyonidae, but is absent in the Miacidae.

ORBITO-TEMPORAL REGION: (FIGURES 14–18.) A primitive feature of the creodonts, exhibited by most Eocene mammals, is the shortness of the frontals, extending back no farther than the point where the supraorbital crests meet. In contrast to the Fissipedia, in

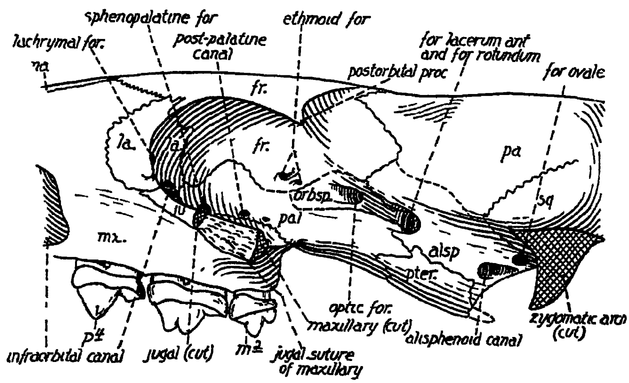


FIGURE 18. Orbital region of *Thinocyon velox*; restored from Amer. Mus. No. 13081, twice natural size.

which the frontals are longer and the brain is larger, these bones cover only the olfactory bulbs, and in large forms, such as *Patriofelis*, where the brain is relatively small, they may not cover the brain at all. Frontal sinuses are present in all except the smallest forms, but are simple. The Limnocyoninae have small, slightly projecting postorbital processes on the frontals, but in the Oxyaenidae they are much reduced, blunted, and do not project at all. The supraorbital or temporal crests are on the dorsal surface of the skull in the Limnocyoninae, but in the Oxyaenidae they form the edge between the dorsal and lateral surfaces. The anterior edge of the orbit is above the posterior part of P^4 in most of this group; in the very short-faced *Patriofelis*, *Sarkastodon* and *Palaeonictis* it is slightly farther forward. The orbit is placed more posteriorly in the long-faced carnivores, such as the Mesonychidae.

The lateral surface of the orbito-temporal region is most completely known in *Thinocyon* (FIGURE 18) and *Oxyaenodon*. The resemblance of these forms to *Sinopa* is very close, and no important differences were observed in the Oxyaenidae. The arrangement is essentially that of the fissipedes, but there are some minor differences. In *Thinocyon* the lachrymal is more extensive in the orbit, as well as on the face; the frontal sends a lobe, lacking in the Fissipedia, between

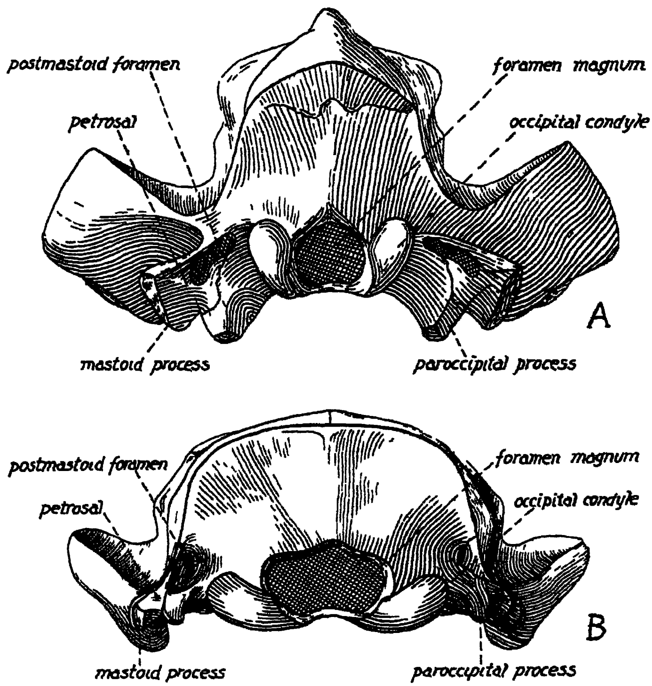


FIGURE 19. Occipital view of skull. A. *Patriofelis ferox*, Amer. Mus No. 1507, three eighths natural size. B. *Thinocyon velox*, Amer. Mus. No. 13081, twice natural size.

the lachrymal and palatine; the alisphenoid-parietal suture is long, whereas it is short in the fissipedes due to the greater extent of the frontal bone; the pterygoid is larger. Of course, the less expanded cranium of the Creodonta gives a different configuration to this region.

The great extent of the parietals appears to be a primitive character, for it occurs generally in the Creodonta. These bones extend from the occipital crest anteriorly to the interorbital constriction, and laterally well down on the side of the cranium, and cover most of the brain. In the fissipedes these bones are relatively smaller and part of their

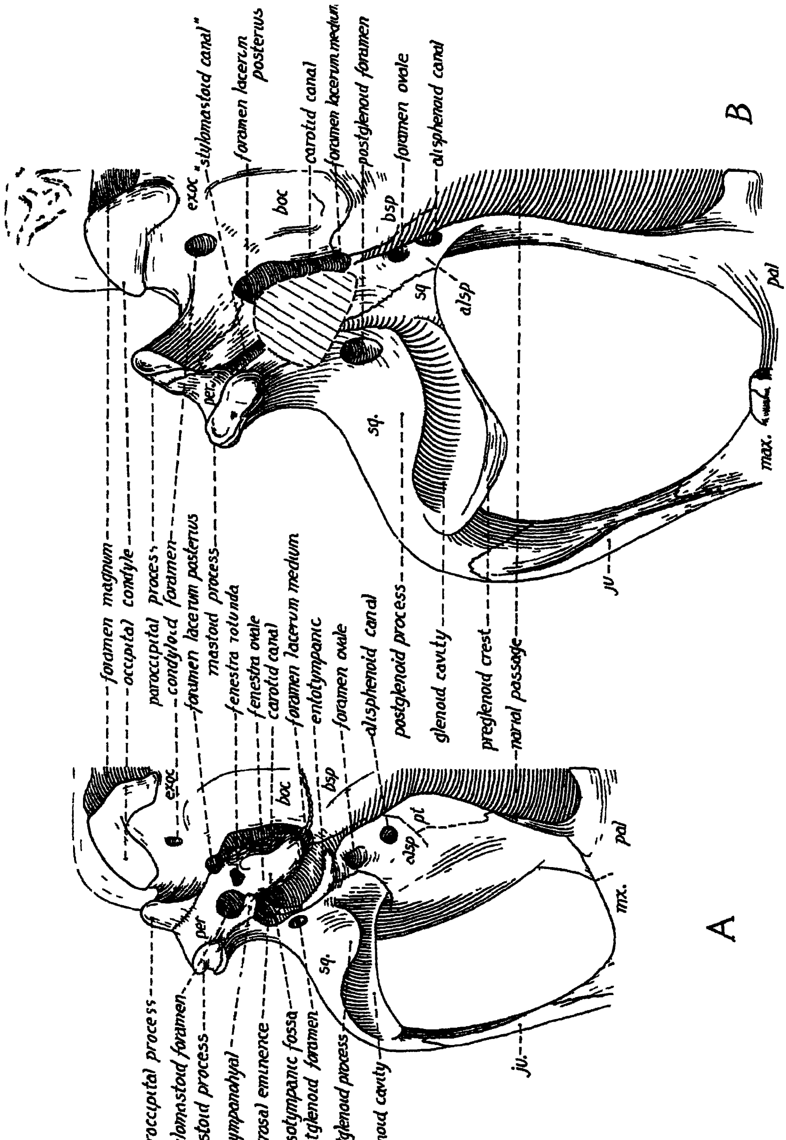


FIGURE 20 Basicranial region A. *Thinocyon velox*, Amer. Mus No 13081 restored, twice natural size. B. *Patriofelis ferox*, restored from Amer. Mus. No. 13145 and No 1507, half natural size

function is taken over by the squamosals and frontals. The sagittal crest is exceedingly high in *Patriofelis*, and very insignificant in the small, weak *Thinocyon*. Its height is correlated with the size and

robustness of the animal and with the relative size of the brain, which is very small in the larger animals, and large in the smaller forms. The supraoccipitals extend onto the dorsal surface of the skull. In front of them, in the parietals, some forms show one or two postparietal foramina.

The zygomatic arch, as the place of origin of the masseter muscle, gives a clear indication of the power of the jaw. In the slender-jawed *Thinocyon* the zygomatic arch is exceedingly thin and weak, while in *Limnocyon* and especially *Oxyaenodon* it is somewhat deeper and more robust, indicating greater crushing power, as the heavier jaw would imply. In *Oxyaena platypus* the zygomatic arch is weak, but in advanced species of *Oxyaena* and in *Palaeonictis* it is robust and deepened, especially in the posterior or squamosal part. The heaviest zygomatic arches are found in *Patriofelis* and *Sarkastodon*, which must have had extremely powerful jaw action. The abrupt deepening in the squamosal part is quite characteristic of the Oxyaenidae and does not occur in the Limnocyoninae. The greatly bowed-out zygomatic arch of *Patriofelis* allows room for a large and powerful temporal muscle.

BASICRANIAL REGION: (FIGURE 20.) The basicranial region of *Limnocyon* and *Thinocyon* has been described in detail by Matthew (1909, p. 435 and 451), who showed the essential similarity with the Fissipedia and other Creodonta, and the primitive character as indicated by the absence of a completely ossified auditory bulla and the probable presence of both external and internal branches of the internal carotid artery. However, as van der Klaauw pointed out (1931, p. 17), in its primitive state the auditory bulla is loosely attached to the skull, and its absence may mean only that it has not been preserved. A horizontally placed annulus tympanicus, incomplete laterally, is present in *Oxyaenodon* (Carn. Mus. No. 3051) and a fragment of it is preserved in one specimen of *Thinocyon* (Amer. Mus. No. 12631); it is probable that it occurred in most creodonts, but since it is loosely attached, has been preserved only rarely.

The form of the petrosal prominence is pear-shaped, tapering anteriorly in the Limnocyoninae. In *Oxyaenodon* it is crested ventrally where it meets the tympanic ring. It is unknown in the Oxyaenidae.

The facial nerve leaves the skull of the Limnocyoninae through the foramen stylomastoideum primitivum. This is bounded anteriorly by a small process extending from the base of the mastoid process to the petrosal eminence. Matthew (1909, p. 451) considered this to be a spur of the post-tympanic process of the squamosal, but it appears to

be a part of the petrosal, suturally separated from the squamosal. As van der Klaauw suggests (1931, p. 172), this may represent the tympanohyal which usually bounds the stylomastoid foramen anteriorly. On the ventral surface, between the paroccipital and mastoid processes of *Patriofelis* is a groove, starting at the position of the

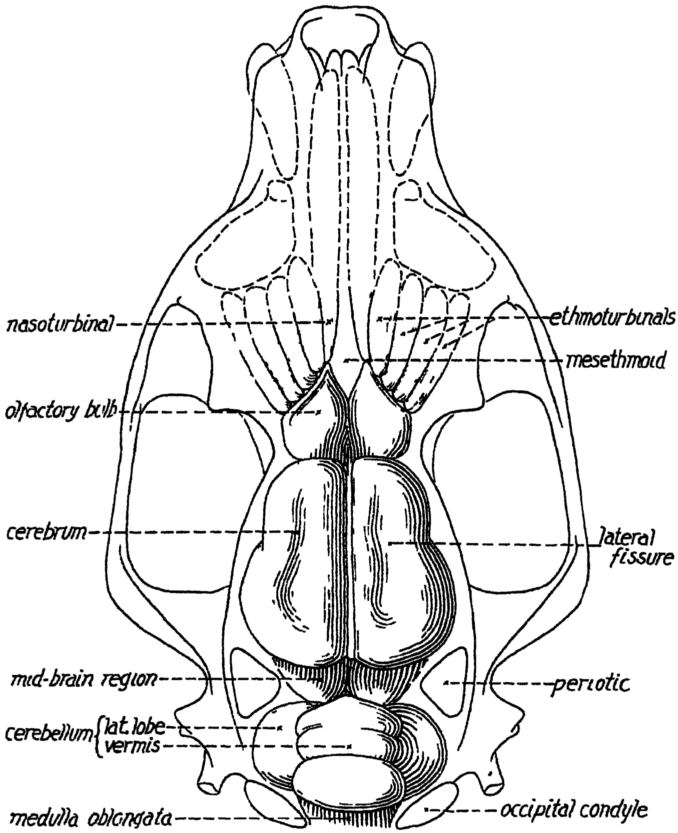


FIGURE 21. Brain of *Thinocyon velox*, restored from Amer. Mus. No. 12631, three halves natural size.

primitive stylomastoid foramen of *Thinocyon*. This groove may represent the "stylomastoid canal" or the external part of the aquaeductus Fallopii. If this is true, an ossified auditory bulla was present probably in *Patriofelis*, and the facial nerve left the skull through a foramen stylomastoideum definitivum. In this respect *Patriofelis* is more advanced than any of the Limnocyoninae. *Oxyaena* agrees with *Patriofelis* in the presence of the "stylomastoid canal."

The paroccipital process of the Limnocyoninae is flat, spatulate, and backwardly directed as in *Sinopa*. It is slender in *Thinocyon* and slightly heavier in *Limnocyon* and *Oxyaenodon*. In the Oxyaenidae it is more robust and downwardly directed.

A post-glenoid process is present invariably in the Creodonta. The Oxyaenidae have a preglenoid crest, as do the Mesonychidae and Triisodontinae. All the other creodonts, including the Limnocyoninae lack this crest. This is an important distinction between the two groups of broad-skulled Pseudocreodi.

The structure of the basicranial region of *Prolimnocyon*, which has never been described, is shown in part in Amer. Mus. No. 15171. It agrees very closely with that of *Thinocyon* and *Sinopa*, differing from the former only in the smaller post-glenoid foramen, the presence of a small subsquamosal (?) foramen lateral to the postglenoid foramen, and in the less robust mastoid process.

OCCIPITAL REGION: (FIGURE 19.) The shape of the occipital region varies greatly within this group. In small forms, such as *Thinocyon*, the brain is relatively large, and there is ample space for muscle attachment without the development of sagittal and occipital crests. On the other hand, strong crests are needed to extend the area for muscle insertions in large and powerful forms such as *Patriofelis*, which have relatively small brains.

The petrosal bone has a small extent on the occipital surface above the mastoid process. Its dorsal part extends into a fossa, at the bottom of which is the mastoid foramen for a vein. The fossa and foramen are present generally in creodonts, and usually absent in fissipedes, where the expansion of the brain has filled out this space.

BRAIN: (FIGURE 21.) The brain, whose form is best known in *Thinocyon velox* (Amer. Mus. No. 12631), is of the same primitive type exhibited by all the Eocene creodonts. The olfactory lobes are very large, placed high, and entirely uncovered by the cerebrum. They indicate a predominance of the olfactory sense, which is reduced to a greater or lesser degree in all the fissipedes. These lobes are covered by the frontals in *Thinocyon*. The cerebral hemispheres, which are relatively small and simple, are pear-shaped, or slightly wider posteriorly than anteriorly. They cover the mid-brain region only partly, and show no tendency to override the olfactory lobes. The convolutions, moderately complex in the later fissipedes, are extremely simple here; dorsally, on either side of the median superior longitudinal fissure, there is only a sulcus lateralis; a more lateral groove may represent a rhinal fissure. The cerebral hemispheres are covered en-

tirely by the parietals in all the members of this group; certain of the Miacidae show an advance towards the Fissipedia in that the hemispheres project somewhat under the frontals.

The mid-brain region is not clear. That it is partly exposed, and not completely overridden by the cerebral hemispheres, is a very primitive character. The cerebellum, which in later fissipedes is partly covered by the cerebrum, is entirely exposed, as in all the Eocene carnivores.

The cranial cavity of *Patriofelis* is shown partly in Amer. Mus. No. 1507. Since this is a much larger animal, the brain is relatively smaller, and the olfactory lobes are partly covered by the parietals. Moreover, the roofing bones, which are very thin in *Thinocyon*, are extremely thick in this genus. Although Wortman (1894, p. 134) states there is no tentorium, there appears to be a thick one separating the cerebrum and cerebellum. The structure of the brain is essentially similar to that of *Thinocyon*.

Vertebrae

CERVICALS: The course of the vertebral artery on the atlas appears to be a fundamental character, indicative of family or superfamily relationships. In the Pseudocreodi and Mesonychidae, this artery passes around the anterior end of the transverse process in a very shallow groove. In the Canidae, Felidae, Procyonidae and *Miacis* (Miacidae) this groove is deep, while in the Ursidae, Mustelidae, Viverridae, Hyaenidae and *Oodectes* (Miacidae) it is bridged over to form a foramen. The formation of the deeper groove or foramen is correlated with the widening antero-posteriorly of the transverse process, which is narrow in the Pseudocreodi.

The posterior six cervicals are of the usual carnivore type. The spine of the axis extends anteriorly over the atlas, and has also a more slender posteriorly directed process. The spine is small or absent on the third cervical, but beginning with the fourth, the spines increase in height posteriorly. Spines are higher and more robust in the heavy-skulled *Patriofelis*, intermediate in *Limnocyon* and *Oxyaena*, and somewhat weaker in *Thinocyon*. The transverse processes of the anterior cervicals are simple, but those of the fifth and sixth, and probable the fourth also, are divided into superior and inferior lamellae, while the seventh retains only the superior lamella, and lacks the vertebrarterial canal.

The adaptation of the cervicals, as judged by general form and development of processes, agrees most closely with *Procyon* and *Nasua* among modern carnivores.

THORACI-LUMBARS: Although individual variations are not uncommon, the number of thoraci-lumbar vertebrae in fissipedes is generally twenty, and this is probably the usual number in the Creodonta. In the Oxyaenidae, *Oxyaena* is known to have twenty, while in the Hyaenodotidae, *Sinopa, Tritemnodon* and *Hyaenodon* have the same number. Other Pseudocreodi have this region incompletely known. The majority of the Fissipedia have thirteen thoracics and seven lumbars, but formulas of 14–6, 15–5, and occasionally 16–4 occur. A thoraci-lumbar formula of 13–7 is probably primitive in the Creodonta; it is found in *Sinopa* and *Oxyaena.* More specialized genera may have the lumbar region reduced; *Patriofelis* and *Tritemnodon* have six, and *Limnocyon potens* only five lumbar vertebrae. Since the lumbar region is the most flexible part of the back, a reduction in the number of lumbar vertebrae would mean that the range of motion of the backbone was correspondingly reduced. In confirmation of this, it appears that most of the cursorial and bounding fissipedes, which bend the back greatly in rapid locomotion, have a long lumbar region with seven vertebrae, while the stiff-backed, ambulatory types usually have only five or six lumbars.

Near the middle of the thoraci-lumbar series is the anticlinal vertebra. Its position varies slightly, but is usually the eleventh thoracic, as it is in *Oxyaena, Sinopa, Tritemnodon,* and probably in *Patriofelis* and *Palaeonictis. Limnocyon potens* agrees with certain of the more heavy-bodied, ambulatory Fissipedia in having the twelfth thoracic anticlinal; its more posterior position is correlated with the shortening of the lumbar region. The anticlinal vertebra is a point of change in the direction of forces. Anterior to it the main pull on the neural spines is from the direction of the head, thus the spines lean backward; posterior to it the main stress is from the opposite direction and the spines lean forward. The anticlinal spine is lower than the others and is vertical. The highest spines are in the anterior thoracic region, since here attaches the ligamentum nuchae, which helps to support the head. These spines are generally higher and stronger in the Creodonta than in the Fissipedia, since the head is relatively larger in the former. They are especially strong in the heavy-headed *Patriofelis.* In the broad-skulled Pseudocreodi, the lumbar spines are relatively low and robust, often expanded at the top, especially so in *Patriofelis* and *Limnocyon potens.* In this they agree with the more heavy-bodied ambulatory fissipedes, such as *Meles, Taxidea* and *Arctictis.*

The anticlinal vertebra is also a point of change in motion. Ante-

riorly, in the chest region, motion is relatively slight, and the zygapophyses are simple, flat or slightly concave and convex, and placed in a nearly horizontal plane. There is an abrupt change at the posterior zygapophyses of the anticlinal vertebra to a more complex type of articulation. The function of these complex zygapophyses is to prevent any dislocation as a result of the greater and more varied movements in the lumbar region. The simplest type of posterior thoracic and lumbar zygapophysis (FIGURE 22A) is found in the Miacidae and Fissipedia; here the articulatory surface of the posterior zygapophysis is moderately convex, and faces laterally and downwards; the anterior zygapophyses are concave and face inwards and upwards. The majority of the Creodonta, including the Hyaenodontidae,

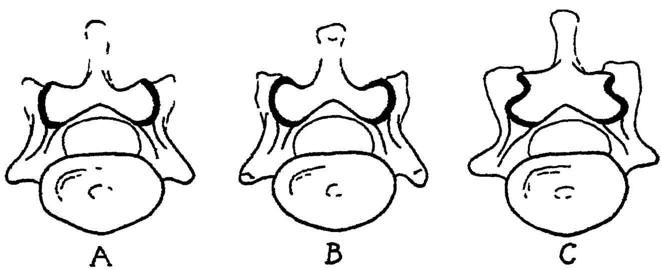


FIGURE 22. Posterior view of lumbar vertebrae, showing extent of articulatory surface of posterior zygapophyses in heavy line. A Type found in Miacidae and Fissipedia. B Type found in *Limnocyon*. C. Revolute zygapophyses of *Patriofelis*

primitive Oxyaenidae, Mesonychidae and some Arctocyonidae, have a more complex articulation of a tongue and groove type (FIGURE 22B). This differs from the miacid type in that the articulatory area of the posterior zygapophysis is extended onto the dorsal surface. *Dissacus*, an early mesonychid, and the primitive hyaenodontids *Sinopa*, *Thinocyon* and probably *Prolimnocyon*, are intermediate to the miacid type in that the dorsal extent of the articulatory surface is slight. *Patriofelis* has a highly complex, concavo-convex lumbar articulation (FIGURE 22C), termed "revolute" by Osborn (1900, p. 274). An incipient stage in the development of revolute articulation is seen in the posterior thoracics and anterior lumbars of advanced *Oxyaena*, *Palaeonictis*, *Limnocyon potens* and later mesonychids. The obvious function of revolute zygapophyses is to prevent torsion, but the reason for its occurrence in *Patriofelis* and absence in other creodonts is not clear. The fact that a similar type of articulation is present in certain artiodactyls suggested to Cope (1889, p. 211) that it was correlated with a trotting gait.

Behind the anticlinal vertebra, the centra and neural arches are lengthened and broadened, and the small metapophysis of the anterior thoracics becomes divided into large, distinct an- and metapophyses. The transverse or costal processes do not appear until the first lumbar vertebra. They are relatively short and robust in the broad-skulled Pseudocreodi, especially so in *Patriofelis;* this is another indication of an ambulatory gait. *Limnocyon potens* is peculiar in that the spinal nerves leave the anterior thoracic vertebrae through a foramen in the pedicel, rather than through a notch.

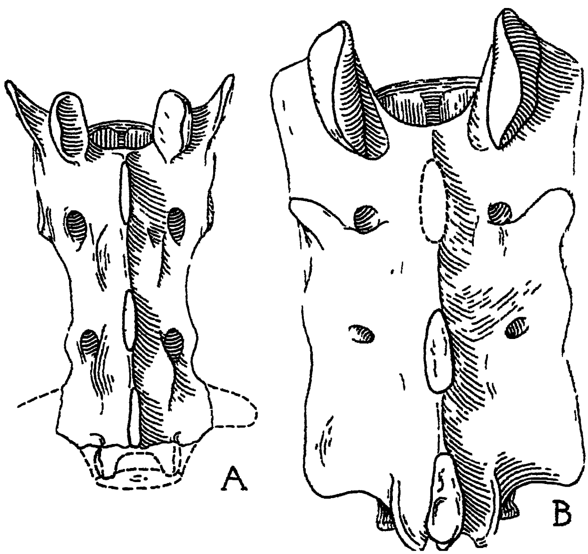


Figure 23. Dorsal view of sacrum. A *Thinocyon velox*, Amer Mus No. 13081, twice natural size B *Patriofelis ferox*, Amer Mus No. 1507, half natural size.

SACRUM: (Figure 23.) The members of this group have three sacral vertebrae, the usual number in fissipedes, and probably the primitive number for creodonts. The anterior zygapophyses are of the lumbar type, whereas the posterior are much more simple. The lateral mass, to which the pelvis is fastened, arises largely from the first sacral vertebra, but in *Patriofelis*, *Palaeonictis*, and *Limnocyon potens* it is supported to some extent by the second, indicating perhaps a stronger pelvic attachment. In the Limnocyoninae there is an anterior process from the lateral mass, entirely distinct from the anterior zygapophysis, which increases the area for attachment. In the presence of this process the Limnocyoninae resemble other Hyaenodontidae and the Miacidae, and differ from the Oxyaenidae and

Mesonychidae, in which it is entirely lacking. The transverse costal processes of the Limnocyoninae are essentially like those of *Tritemnodon;* the first forms the lateral mass, the second is barely indicated, and the third is wide and distinct. In *Patriofelis* and probably in *Oxyaena* they are all united indistinguishably, and are not widely expanded laterally.

CAUDALS: All the creodonts which are not especially adapted for running are characterized by a relatively longer and stronger tail than is present in most fissipedes. Powerful transverse processes are present on the anterior caudals, but are reduced in size posteriorly, and become subdivided into anterior and posterior processes on the seventh or eighth caudal. A primitive feature is that the neural canal is enclosed for a considerable distance, up to the ninth caudal in *Patriofelis*, to the tenth in *Limnocyon*, and to the twelfth in *Tritemnodon*. The number of caudal vertebrae, though not known exactly in many creodonts, is large. Twenty-six are preserved in *Patriofelis* (Amer. Mus. No. 1507), and there may have been twenty-eight or more.

It is impossible to tell from the vertebrae alone whether the tail was prehensile. It probably was in some of the Miacidae which were almost certainly arboreal. In most of the Pseudocreodi, however, the long, powerful tail was merely an inheritance from arboreal ancestors (Matthew, 1904) and had lost its power of prehension.

Ribs

In the Pseudocreodi, there are thirteen ribs on each side in *Oxyaena*, *Sinopa* and probably *Palaeonictis*, fourteen in *Hyaenodon*, *Tritemnodon* and *Patriofelis*, and probably fifteen in *Limnocyon potens*. Of these, the last two to four lack the tuberculum. The first rib is short, wide and flat, but the other ribs are rounder in section, or less flattened than is usually the case in fissipedes. *Patriofelis* has heavy ribs, widely bowed-out to form a robust thorax such as occurs in the heavier and more ambulatory fissipedes. *Oxyaena* has more slender ribs and thorax, but the latter is not compressed as it is in cursorial carnivores. *Thinocyon* has relatively slender ribs.

Sternum

The manubrium of *Thinocyon* (Amer. Mus. No. 11524) and *Limnocyon* (Amer. Mus. No. 13138) is similar to that of *Tritemnodon*. Anterior to the facet for the first sternal rib it is broad, flat dorsoventrally, and thin; posteriorly it is slender and oval in section. In *Patriofelis* the manubrium is of a very different type; it is relatively long, deep and laterally compressed, and the anterior part is not at

all expanded transversely. The mesosternal elements, six in number where known, are relatively short and robust in *Patriofelis* and *Palaeonictis*, and somewhat longer, more slender, and slightly constricted in the middle in *Thinocyon*, *Sinopa*, and *Tritemnodon*. The xiphisternum was not preserved in any of the specimens examined, and was probably cartilaginous.

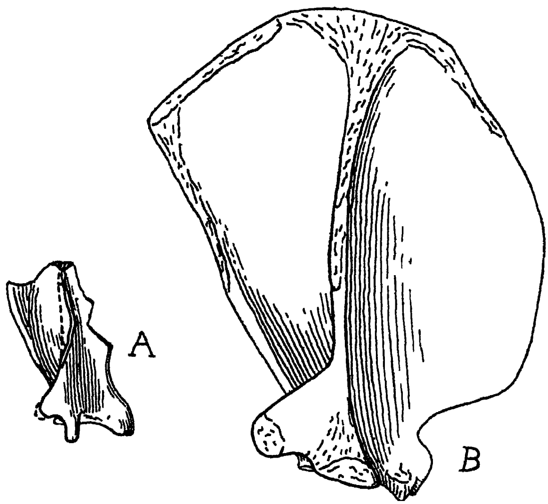


Figure 24. Lateral view of right scapula. A. *Thinocyon medius*, Amer. Mus No 12154 four thirds natural size. B *Patriofelis ferox*, Amer. Mus. No 1508, one third natural size

Fore Limb

SCAPULA: (Figure 24.) The scapula is well known in the broad-skulled Pseudocreodi only in *Patriofelis*. The fragmentary remains resemble other creodonts in the following characters which may be regarded as primitive for the Carnivora: subequal supra- and infraspinous fossae; well developed, projecting acromion; prominent metacromion; and distinct, projecting coracoid. The only creodont in which a clavicle has been determined is *Tritemnodon*, where it is much less reduced than in any recent carnivore. The relatively long acromion, to which this bone is attached, suggests a correspondingly large clavicle in the Limnocyoninae; *Patriofelis* has a relatively shorter and broader acromion, but it is a safe inference that the clavicle was better developed than in any fissipede.

The differences between the scapulae of the Limnocyoninae and Oxyaenidae are due largely to different adaptation. The Limnocyoninae, especially *Thinocyon*, agree with *Sinopa* and other semi-

cursorial types in having a relatively narrow scapular blade, shallow fossae, and weaker spine, acromion, and metacromion. The Oxyaenidae, especially *Patriofelis*, have a much broader blade, deep fossae, high spine, and robust acromion and metacromion. This type of scapula is approximated most closely among the more ambulatory fissipedes, such as *Nasua*. *Oxyaena*, *Palaeonictis*, and *Oxyaenodon* are of an intermediate type.

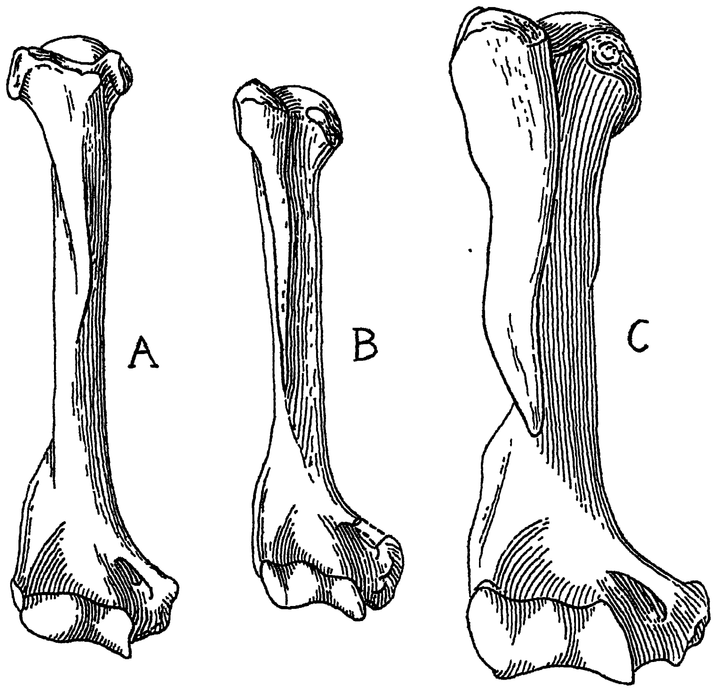


FIGURE 25. Anterior view of right humerus. A. *Thinocyon medius*, Amer. Mus. No. 12154, four thirds natural size. B. *Oxyaena platypus*, Amer. Mus. No. 15857, two thirds natural size. C *Patriofelis ferox*, Amer. Mus. No. 1507, one third natural size.

HUMERUS: (FIGURE 25.) The primitive creodont humerus was moderately short and robust, with a prominent, massive greater tuberosity, strong lesser tuberosity, high deltoid and supinator crests, wide entepicondyle with a large foramen, small ectepicondyle, shallowly grooved distal articulatory surface, and shallow olecranon fossa. Such a humerus is found generally in Paleocene Creodonta, and occurs in *Oxyaena* and *Limnocyon*. Comparison with recent carnivores indicates that it belongs to an essentially ambulatory type.

The Limnocyoninae and Oxyaenidae differ in the form of the deltoid

crest. In the former it tapers off gradually at about the middle of the shaft; in the latter it extends nearly two thirds of the length of the shaft and ends abruptly. It is moderately high and robust in *Limnocyon* and in small species of *Oxyaena*, more strongly developed in *Palaeonictis* and in larger *Oxyaena*, and exceptionally high and wide in *Patriofelis*, indicating extremely powerful pectoral and deltoid

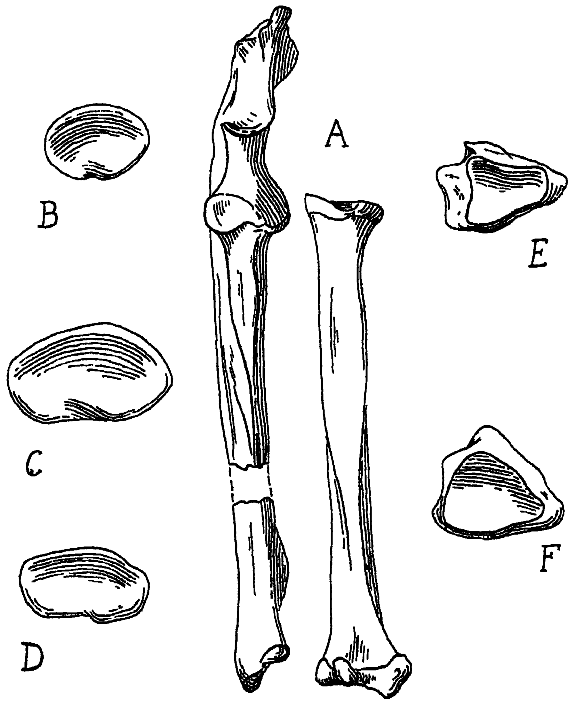


Figure 26. A. *Oxyaena platypus*, anterior view of right radius and ulna, Amer. Mus. No. 15857, natural size. B–D. Proximal view of right radius; B. *Oxyaena platypus*; C. *Patriofelis ferox*; D. *Limnocyon verus*. E–F. Distal view of right radius: E. *Oxyaena platypus*; F. *Limnocyon verus*

muscles. On the other hand it is relatively low and weak in *Oxyaenodon*, more so in *Thinocyon* and *Thereutherium*; this is partly due to smaller size, and partly to a more cursorial type of locomotion.

The shallow olecranon fossa and fairly deep anterior supratrochlear fossa of *Patriofelis* show that the elbow-joint was quite angulate and could not be straightened entirely under ordinary circumstances. This considerable angulation is a clear indication of an ambulatory gait, and together with the large size of this form, explains the extremely

robust crests and processes for the attachment of muscles, which function as much to support as to move the animal. The olecranon fossa of the Limnocyoninae, especially of *Thinocyon*, *Machaeroides*, and *Oxyaenodon*, is deeper than in the Oxyaenidae, signifying either a greater range of motion at the elbow or a less angulate limb. In any case, a more cursorial type of locomotion is certain. The different gait and smaller size account for the more slender crests and processes for muscle attachment.

The distal articulatory surface is relatively wide and shallow in the broad-skulled Pseudocreodi, as in primitive creodonts generally. In the Oxyaenidae the trochlear surface for the ulna is of small antero-posterior extent, and is very shallowly grooved, indicating a limited range of motion. The Limnocyoninae, especially *Thinocyon* and *Oxyaenodon*, approach more cursorial types in having a more deeply grooved trochlear surface, which is extended farther into the anterior supratrochlear and olecranon fossae; this allows a greater range of motion, but restricts it to a more antero-posterior direction.

RADIUS: (FIGURE 26.) The radius of the broad-skulled Pseudocreodi is moderately robust, with the shaft somewhat curved in the typical carnivore manner. The head of the radius is round-oval in *Oxyaena platypus* and *Thinocyon*, indicating that these forms retained to a considerable degree the power of pronation and supination that the ancestral arboreal placentals possessed (Matthew, 1904, p. 813). However, since it may be only a heritage character, it is, by itself, no proof that the habits of these two forms were arboreal. The radius of the other Oxyaenidae has moderately to very wide-oval heads, which allows little twisting on the ulna. In *Limnocyon*, *Oxyaenodon* and some species of *Oxyaena* this is correlated with the assumption of a more cursorial gait.

The distal articulatory surface for the scaphoid and lunar bones is quite wide antero-posteriorly, and shallowly convex; it restricts movement little at this joint. There may be a small contact with the cuneiform, at least in some of the Pseudocreodi.

ULNA: (FIGURE 26A.) The ulna agrees with that of other primitive creodonts in having a robust shaft, flattened dorso-ventrally at the distal end, but unreduced and freely movable on the radius. A more or less ambulatory gait is indicated by the long olecranon which furnishes a moderately strong lever-arm for M. triceps brachii, allowing powerful but relatively short motions of the forearm. This process is especially long and robust in *Patriofelis*, and is shortest in *Thinocyon* and *Oxyaenodon*, which are more cursorial. The upturning

of the olecranon, which is found in creodonts generally, means that less straightening of the elbow-joint is possible. In cursorial forms, which have less motion at the shoulder-joint and more at the elbow, the olecranon tends to be downturned to allow a greater range of motion.

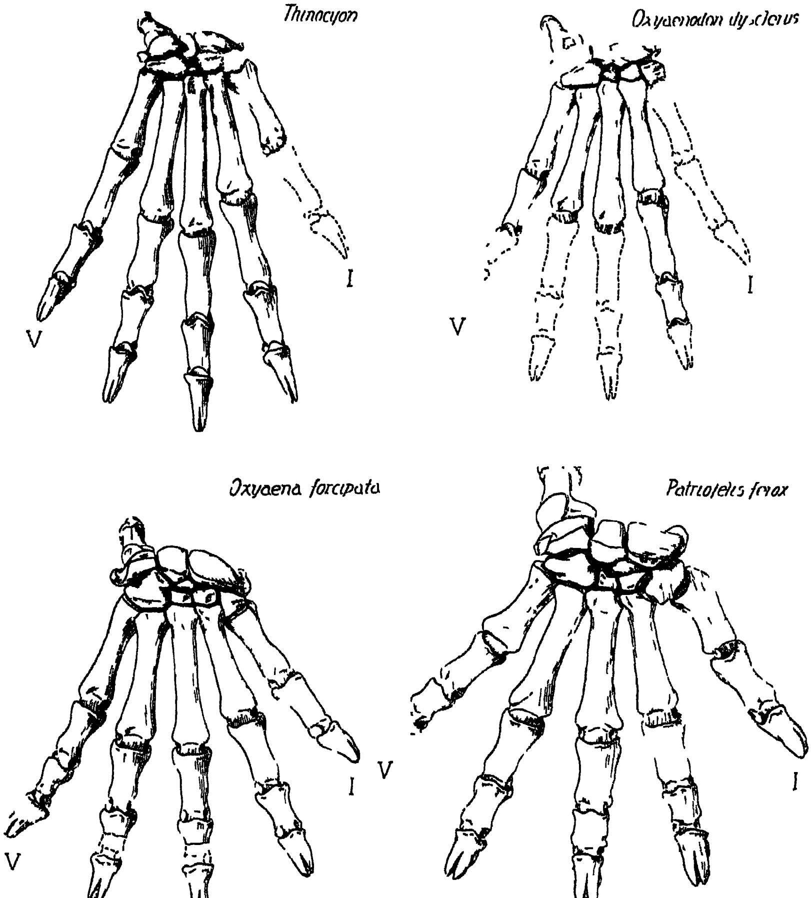


FIGURE 27. Restorations of right manus of the broad-skulled Pseudocreodi

The proximal end of the olecranon lacks a distinct groove in most of the broad-skulled Pseudocreodi; in *Thinocyon* and *Oxyaenodon*, and to a greater extent in truly cursorial forms, there is a marked groove for the tendon of the caput longum of M. triceps brachii, since there is greater motion of this tendon over the olecranon in the latter forms.

Most creodonts have the olecranon twisted inwardly, and the semilunar notch placed obliquely to the axis of the shaft. This obliquity is greater in the Limnocyoninae than in the Oxyaenidae. It means that the forearm is not in the same vertical plane as the humerus, but that the distal end of the ulna is directed somewhat outward relative to the humerus. The articulatory surface for the trochlea of the humerus is relatively wide, and only slightly convex laterally. In truly cursorial forms motion at the elbow-joint is limited to a more strictly antero-posterior direction by a greater convexity of this surface and a corresponding deeper grooving of the trochlea of the humerus. *Thinocyon* and *Oxyaenodon* approach the cursorial type in this, as in other respects. The lesser sigmoid notch, or surface for the head of the radius, is only slightly concave in most of the members of this group, in correlation with the wide-oval head of the radius and the reduced power of pronation and supination.

MANUS: (FIGURE 27.) The manus of the broad-skulled Pseudocreodi is of a very primitive type as shown by the following characters: (1) The carpal elements are free, with rare exceptions; the scaphoid and centrale are fused on one side in a specimen of *Limnocyon verus* (Amer. Mus. No. 12155); the scaphoid, centrale, and lunar are united in *Oxyaenodon dysclerus* (Carn. Mus. No. 3051). Such fusions occur as individual variations in occasional Paleocene and Lower Eocene Creodonta, and are general in the later Miacidae and Fissipedia. (2) The carpus is of an alternating or interlocking type, with the lunar resting almost equally on the centrale, magnum and unciform. (3) The pollux is large and more or less divergent as indicated by the convex and somewhat inwardly facing facet on the large trapezium; this character is found in many Paleocene and Eocene mammals, and according to Matthew (1904) is inherited from arboreal placental ancestors. (4) The ungual phalanges are cleft. Since this character is found in most of the Creodonta and several other early groups of mammals, it is probable that it is a primitive character which has been lost in such forms as the Miacidae where the terminal phalanges are much compressed laterally.

The manus of the Limnocyoninae differs from that of the Oxyaenidae and resembles that of the Hyaenodontidae in several rather fundamental points. This resemblance is so close that two forms which are adaptively similar in the limbs, *Limnocyon* among the Limnocyoninae, and *Tritemnodon* among the Proviverrinae, are hardly distinguishable from the foot alone. The lunar-unciform contact is large in the Oxyaenidae, small in the Limnocyoninae. The anterior,

non-articular face of the magnum is moderately large in the Oxyaenidae, very small in the Limnocyoninae. The unciform is deep proximodistally in the Oxyaenidae, whereas it is shallow and wide transversely in the Limnocyoninae. The radial articulatory surface of the scaphoid has a very characteristic posterior expansion on the ulnar side in the Oxyaenidae, entirely lacking in the Limnocyoninae. The trapezium is relatively larger and broader in the Oxyaenidae. The ungual phalanges are flattened dorso-ventrally in the Oxyaenidae, whereas they are somewhat laterally compressed in the Limnocyoninae. The difference in proportions is more adaptive; the foot is relatively robust, short, and spreading in the Oxyaenidae, while it is longer and more slender in the Limnocyoninae.

Matthew (1909, p. 324) considered the symmetry of the foot to be an essential difference between the Miacidae and Mesonychidae which he called paraxonic, and the Pseudocreodi which he called "approximately mesaxonic." The paraxonic symmetry of the later, highly cursorial Mesonychidae is obvious, but the differences between the symmetry of the feet of the other families is less clearly marked. If subequal digits III and IV, and shorter digits II and V indicate a paraxonic foot, *Oxyaena*, *Patriofelis*, and *Palaeonictis* are nearly as paraxonic as any of the Miacidae. But the difference is so small from the early Hyaenodontidae in which digit III is longest, and II and IV are slightly shorter and subequal, that it can hardly be considered fundamental, especially since the difference is less clearly marked in the hind foot. The mesaxonic symmetry of the Hyaenodontidae is even less certain, since metacarpal IV is appreciably longer than III. In the absence of any marked difference in the carpus, it appears that the primitive symmetry of all the Creodonta, including the Paleocene Mesonychidae, is fundamentally similar, and intermediate between paraxonic and mesaxonic.

The manus of the broad-skulled Pseudocreodi is plantigrade to subdigitigrade, indicating an ambulatory to subcursorial manner of locomotion. *Patriofelis* is the extreme of the plantigrade type as shown by the following characters: (1) Foot robust, short and spreading. (2) Carpus short proximo-distally, with the elements articulating loosely to allow relatively free and varied movements. (3) Radial articulatory surface of scaphoid extending so far anteriorly that it nearly meets the distal articulatory surface; this implies an angulation between the forearm and wrist which is not found in cursorial types. (4) Pisiform short and robust. (5) Digits I and V relatively long. (6) Metacarpals and proximal phalanges short. (7) Metacarpals

spreading and articulating loosely. (8) Distal articulatory surface of metacarpals lacking any distinct fossa above it; this is an important character, indicating that the angulation between the metacarpals and proximal phalanges is slight. In digitigrade forms the articulatory surface is more sharply convex and is continued into a distinct fossa above it anteriorly, so as to make possible a greater angulation at this joint.

Palaeonictis and *Oxyaena platypus* are also extremely plantigrade forms, while *Limnocyon* and the other species of *Oxyaena* are slightly less so, judging from the above criteria. *Thinocyon* and *Oxyaenodon*, relatively small, light-limbed forms, might be classed as subdigitigrade. The foot is relatively longer and more slender; the pisiform is longer; digits I and V are slightly reduced; the metacarpals and proximal phalanges are longer, and the former articulate more compactly; the distal articulatory surface of the metacarpals is more sharply convex and has a small fossa above it.

Hind Limb

PELVIS: (FIGURE 28.) The pelvis of the Oxyaenidae is characterized especially by the great dorsal expansion of the upper part of the ilium, and by the extremely strong lateral ridge which bounds it ventrally. Since this is the area of origin of the gluteal muscles, the latter must have been exceptionally strong. The gluteal muscles abduct and rotate the femur, and their great development signifies varied motions of the latter bone, as opposed to the more strictly antero-posterior motion of cursorial types. This characteristic expansion of the dorsal plate of the ilium is found also in the Hyaenodontidae and primitive Mesonychidae, but to a lesser degree; it is not known in other Carnivora. The lateral ridge on the ilium is developed less strongly in the Limnocyoninae than in the Oxyaenidae, and is only faintly marked in the small, light-limbed *Thinocyon*. The expansion of the ventral part of the lateral face of the ilium is also correlated with varied femur motions, since it is here that M. iliacus has its origin. The strong iliac crest and the eversion of the anterior end of the ilium indicate powerful back muscles (M. longissimus dorsi), especially in the Oxyaenidae.

The cotyloid notch in the acetabulum, through which passes the ligamentum teres, is a good indicator of the manner of locomotion. In truly cursorial types it is deep and narrow; in ambulatory, and especially arboreal types, where femur movements are varied, it is relatively shallower and wider, allowing freer motion. In most of the

broad-skulled Pseudocreodi it is moderately shallow and open, agreeing approximately with *Procyon* among the fissipedes; it is slightly deeper and narrower in *Oxyaena platypus* and *Thinocyon*, resembling *Felis* in this respect.

The ischium is slightly longer in the Limnocyoninae than in the Oxyaenidae, and as a result the obturator foramen is longer-oval in the former. In none is the ischium as long as the ilium, for it is es-

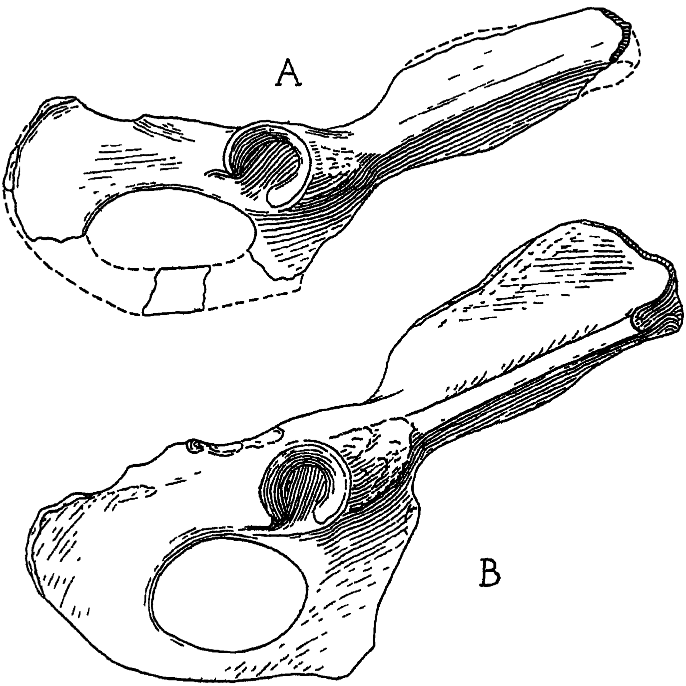


FIGURE 28. Lateral view of right pelvis. A. *Limnocyon potens*, Amer. Mus. No. 13138, two thirds natural size. B. *Patriofelis ferox*, Amer. Mus. No. 1508 one third natural size.

pecially in leaping and running forms that the ischium is elongate. The ischial spine is strong, especially in the Oxyaenidae; its great development is correlated probably with the large size of the tail. The pubic symphysis is of moderate length, but is not especially strong.

FEMUR: (FIGURE 29.) The femur of the broad-skulled Pseudocreodi has the following characters in common with all primitive Creodonta: moderately robust proportions; greater trochanter high, massive; lesser trochanter strong and placed on the mesial side of the

shaft; third trochanter well developed; and trochanteric fossa deep. The proportions are especially robust in the larger forms, and therefore in the Oxyaenidae. The femur of *Palaeonictis* is incompletely known, but is probably considerably longer than restored by Sinclair and Jepsen (1929, FIGURE 1). The shaft of the femur in the Pseudocreodi and Mesonychidae has a peculiar curvature so that its axis passes through the greater trochanter, rather than between the head and the

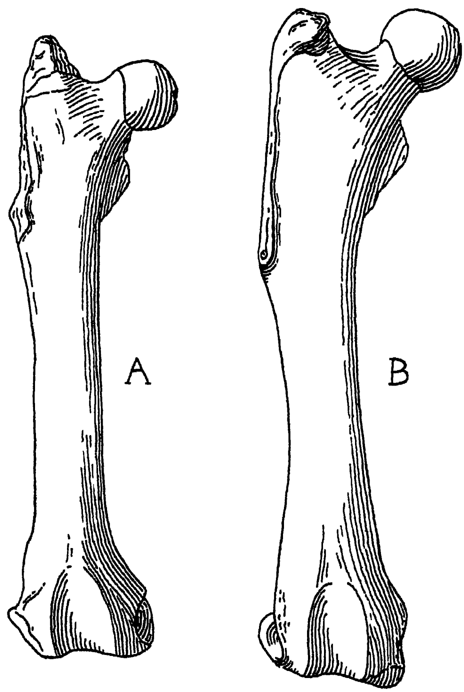


FIGURE 29. Anterior view of right femur. A *Limnocyon potens*, Amer. Mus. No. 13138, two thirds natural size. B *Patriofelis ferox*, Amer. Mus. No 1507, one third natural size.

greater trochanter as in other Carnivora. The strong development of the trochanters and the trochanteric fossa indicate that the muscles which twist, adduct, and abduct the femur are correspondingly powerfully developed, and that this bone is capable of varied movements. The head of the femur in the Oxyaenidae, especially in *Patriofelis* and *Protopsalis*, faces mesio-dorsally, showing that the shaft of the femur was directed somewhat laterally, and that the gait was rather straddling; this suggests a robust body. In the Limnocyoninae the head faces more mesially, and the limb was straighter, and more capable of cursorial locomotion.

It is a general rule, at least among the Carnivora, that the patellar trochlea is relatively long, narrow, and deeply grooved, and the patella is small in cursorial forms. In ambulatory types, the trochlea is shorter, broader, and more shallowly grooved, and the patella is relatively long, wide, and robust. The extensor of the tibia, M. quadriceps femoris, which has its insertion on the patella, and whose

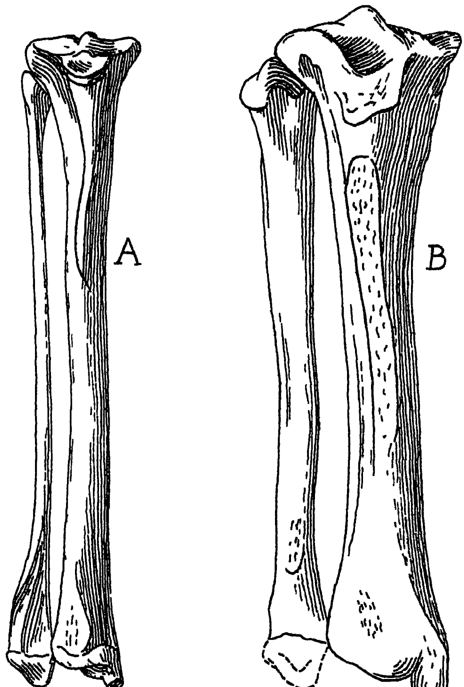


FIGURE 30. Anterior view of right tibia and fibula. A. *Thinocyon velox*, Amer. Mus. No. 13082, four thirds natural size B. *Patriofelis ferox*, Amer. Mus. No. 1507, four ninths natural size.

pull is extended to the tibia by the ligamentum patellae, is a more slender muscle with a faster action at poorer leverage in the cursorial types; it is a larger muscle with a stronger but slower action in ambulatory types. The range of motion of the tendon or patella over the trochlea is also much greater in cursorial forms. Judging by these criteria, most of the Oxyaenidae are ambulatory types, especially *Patriofelis*. The Limnocyoninae, except *Limnocyon*, have a relatively narrower and longer trochlea, and the patella is relatively small. The latter is partly due to the smaller size of the members of this sub-

family, but it is probable that they were sub-cursorial. The condyles and intercondyloid fossa are likewise somewhat deeper in the Limnocyoninae.

TIBIA: (FIGURE 30.) An investigation of the tibia of the primitive creodont leads to the same conclusion as the study of the other limb bones, namely that the early carnivores were rather ambulatory. *Oxyaena platypus* and *Limnocyon* are near to the primitive type and agree in having a low, broad tubercle for the ligamentum patellae, a moderately low and heavy cnemial crest, a shallow fossa for M. tibialis anterior, flat, ungrooved astragalar trochlea, placed obliquely to the axis of the shaft, and a small astragalar facet on the external side of the internal malleolus. The later species of *Oxyaena* have a heavier tibia, and it is exceptionally robust in *Patriofelis* and *Palaeonictis*. On the other hand, *Thinocyon* has a relatively long, slender, more cursorial type of tibia.

The very low tubercle for the ligamentum patellae of *Patriofelis* and *Palaeonictis* is characteristic of ambulatory animals; the leverage is such that the pull of the M. quadriceps femoris, transmitted through the patellar ligament, results in a slow but powerful extension of the shank. *Thinocyon* has a higher tubercle, approaching the condition of cursorial carnivores; the movement of the shank may be much more rapid with this arrangement. The cnemial crest is likewise relatively higher and more slender in *Thinocyon*, as in running types generally; it is exceptionally low and massive in *Patriofelis* and *Palaeonictis*. This crest tapers out gradually below the middle of the shaft in all the Oxyaenidae; the Limnocyoninae resemble the early Hyaenodontidae in that the cnemial crest ends more abruptly above the middle of the shaft, and usually has a peculiar emphasis near its distal end. The proximal fibular facet faces almost directly distally in the Oxyaenidae, while it faces much more laterally in the Limnocyoninae and other Hyaenodontidae. The fossa for M. tibialis anterior on the lateral side of the proximal end of the shaft is generally rather shallow in the broad-skulled Pseudocreodi, indicating that this extensor of the foot is not as strongly developed as in running and jumping forms.

The astragalar trochlea is quite flat in all the members of this group. This is a primitive character, inherited from ambulatory ancestors which had relatively free movement at the ankle joint. The only creodonts which develop a deeply grooved astragalar trochlea are the truly cursorial Mesonychidae and later Hyaenodontidae. The internal malleolus, which restricts lateral or twisting movements at the tibio-astragalar joint, has only a small astragalar facet in the early

creodonts. It is somewhat larger and at a sharper angle to the horizontal astragalar surface in the Limnocyoninae than in the Oxyaenidae.

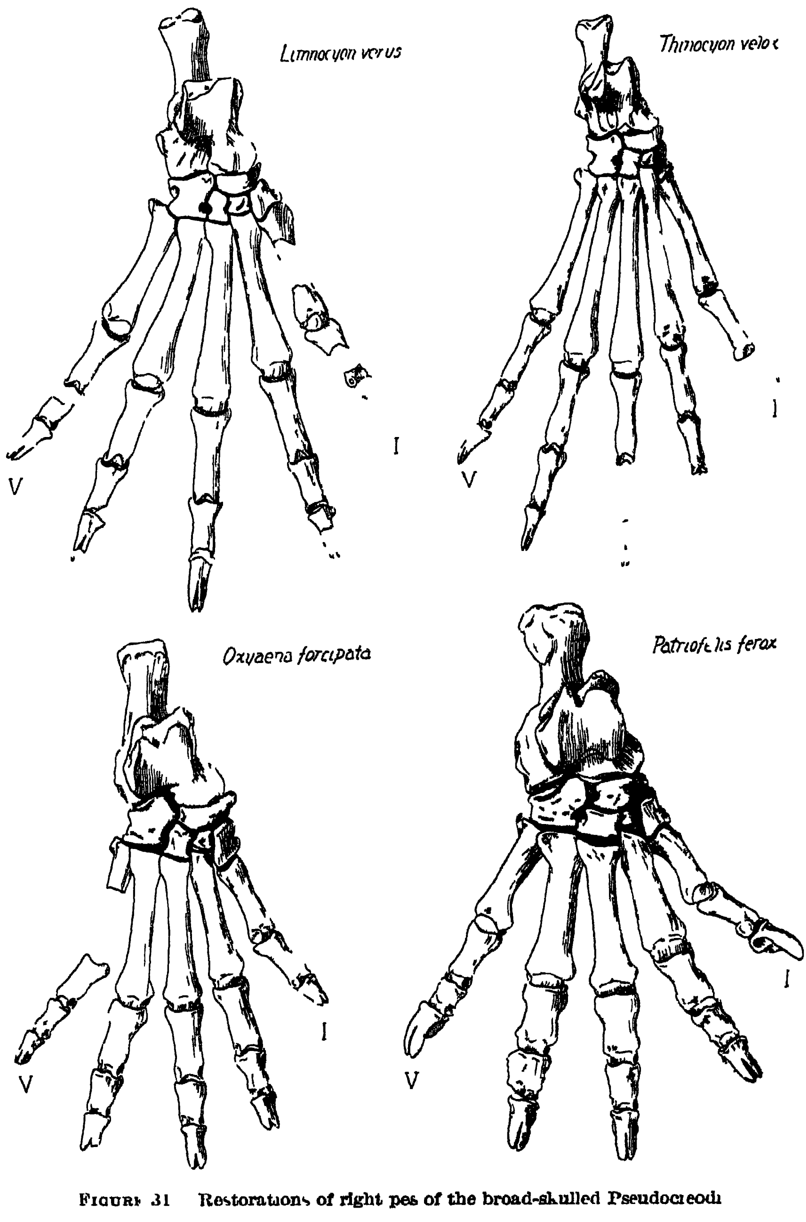


FIGURE 31 Restorations of right pes of the broad-skulled Pseudocreodi

FIBULA: (FIGURE 30.) The fibula is unreduced in the members of this group. In the Oxyaenidae, especially *Patriofelis*, it is very robust, while at the other extreme it is moderately slender in *Thinocyon*. It is freely movable on the tibia; distally there is no distinct facet; the proximal tibial facet faces dorsally in the Oxyaenidae and mesiodorsally in the Limnocyoninae. The distal end, or external malleolus, retains a well developed facet for the calcaneum in the Limnocyoninae. This is a primitive character, found in most creodonts. It is lost in most of the Oxyaenidae, however; a moderate fibulo-calcanear articulation occurs in *Palaeonictis*, none in *Oxyaena;* the very small one in *Patriofelis* is probably secondary. The fibulo-astragalar facet is oblique and may well transmit some of the weight to the fibula.

PES: (FIGURE 31.) Among the characters of the pes which may be considered primitive, the following are important: (1) Foot as a whole plantigrade, pentadactyl, short, and spreading. (2) Tarsus relatively short proximo-distally, and broad. (3) Hallux somewhat divergent, as shown by the unreduced entocuneiform with a saddle-shaped distal articulatory face. (4) Astragalus with body undeepened, trochlea short and only slightly grooved, large astragalar foramen, oblique fibular facet, and wide, flat head. (5) Calcaneum with oblique cuboid facet, and well developed fibular facet; the latter is undoubtedly a primitive character, but has been lost in *Oxyaena*, and the small fibular facet is probably secondary in *Patriofelis*. (6) A cuboid-astragalus contact. (7) The primitive characters of the metapodials and phalanges are the same as in the manus.

The Limnocyoninae closely resemble the Proviverrinae and differ from the Oxyaenidae in several characters. The foot as a whole is shorter, more robust, and spreading in the Oxyaenidae. The body of the astragalus is flat and shallowly convex in the Oxyaenidae, much deeper and more sharply convex in the Limnocyoninae. The trochlear surface of the astragalus is limited to the body in the Oxyaenidae, whereas it extends onto the neck in the Limnocyoninae; it is also less extensive proximo-mesially in the Oxyaenidae. A well developed fibular facet is present on the calcaneum of the Limnocyoninae, whereas it is small or absent in the Oxyaenidae. The astragalus-cuboid contact is large in the Oxyaenidae, and much reduced in the Limnocyoninae. The groove for M. peroneus longus is deep in the Limnocyoninae, and shallow in the Oxyaenidae. The ungual phalanges differ in the same way as in the manus.

Much the same may be said of the symmetry of the hind foot as of the fore foot. Although metatarsals III and IV are subequal in the

members of this group, the symmetry is not truly paraxonic as in the Mesonychidae, for the pressure of metatarsal III is transmitted to both the cuboid and navicular by the wedge-shaped proximal end of the ectocuneiform. In *Thinocyon* the cuboid face of the ectocuneiform is somewhat more vertical, resulting in a more nearly paraxonic arrangement of the tarsus. In any case, the symmetry is not clearly mesaxonic as held by Matthew (1909, p. 324).

The earlier Oxyaenidae, *Oxyaena* and *Palaeonictis*, show every indication of a plantigrade pes. The foot as a whole is short, robust and spreading, with a broad, short tarsus and unreduced and somewhat divergent first digit. The tuber calcis is short and robust. The body of the astragalus is quite flat and the trochlea is very shallowly grooved and of limited antero-posterior extent, while the surface for the internal malleolus is small and at a slight angle to the trochlear surface. The metatarsals are short, spreading, and interlock little; their distal articulatory surface is not sharply convex, and there is little or no depression above it on the anterior face. *Patriofelis* shows an even more complete plantigradism, the foot being excessively short, robust, and spreading, and the tarsus is even more shortened and broadened.

The pes of the Limnocyoninae is longer, more slender and less spreading. There are many indications that it is less plantigrade than that of the Oxyaenidae, but it is probably no more than subdigitigrade, even in the light-limbed *Thinocyon*. The entocuneiform is more reduced than in *Oxyaena*, indicating a less divergent hallux. The tarsus as a whole is deeper proximo-distally and more compact than in the Oxyaenidae. The body of the astragalus is deeper, the trochlear surface longer, and the facet for the internal malleolus more sharply defined than in the Oxyaenidae; but the trochlea is not deeply grooved as in truly cursorial forms. The tuber calcis is relatively longer and more slender than in the Oxyaenidae. The metatarsals are less spreading, and there is a deeper fossa above their distal articulatory surfaces, especially in *Thinocyon*. These characters and many others suggest a subdigitigrade posture for *Thinocyon*, while *Limnocyon* is intermediate to the more plantigrade *Oxyaena*.

ADAPTATION

Feeding Adaptation

Prolimnocyon and *Thinocyon:* These two genera are similar in their small size, long, slender jaws, tuberculo-sectorial lower molars, and relatively slender premolars and canines. Among the Fissipedia

they have their closest analogues in *Viverricula* or *Genetta*, among the Marsupialia, in *Dasyurus*. These recent genera are all largely carnivorous, feeding on small birds and mammals, and it is probable that the diet of *Prolimnocyon* and *Thinocyon* was of a similar nature, although some of the smaller species, such as *T. mustelinus*, may have been insectivorous, or partly so.

Limnocyon is similar in structure to *Thinocyon*, but is larger and has a deeper jaw, and more robust teeth, skull, and jaw, especially in *L. potens*. There are no very close parallels among the Fissipedia; in the Marsupialia, *Sarcophilus* shows many resemblances, but has a much shorter skull and better developed shear. All that can be said is that *Limnocyon* was probably largely carnivorous and capable of crushing bones.

Oxyaenodon differs from *Limnocyon* in its better developed carnassial shear, broader skull, and heavier jaw. In these respects it resembles *Sarcophilus* more closely than does *Limnocyon*. It was a small, but probably powerful carnivorous form, such as *Sarcophilus*.

Thereutherium is a very small form, yet shows every evidence of an extreme carnivorous adaptation in its slender premolars and highly specialized sectorial molars. The fauna of the Phosphorites of Quercy, in which this form occurs fairly abundantly, includes many small mammals and birds on which *Thereutherium* might have fed.

Machaeroides is an extremely carnivorous derivative of the earlier Limnocyoninae showing a close analogy with some of the smaller species of *Felis* in its lower jaw and teeth. The shearing blade of the carnassials is not as well developed as in *Felis*, but is very advanced for a Middle Eocene carnivore. The premolars are slender and shearing, rather than crushing, and are reduced in the anterior part of the jaw. Since the sabre-tooth specializations are only incipient in this genus, its feeding habits were doubtless very similar to those of *Felis*.

Apataelurus is a very close parallel to the true sabre-tooth cats, especially *Hoplophoneus* and *Eusmilus*, differing mostly in the development of $M_{\overline{2}}$ as the main carnassial. Its manner of feeding was similar, without a doubt, to that of the Machaerodontinae. According to Matthew (1910, p. 305) these highly specialized carnivores were adapted for preying on the thick-skinned, slow-moving "pachyderms," which they killed by stabbing, ripping or gashing with their long upper canine tusks. A large element of the fauna of Uinta B, in which *Apataelurus* was found, consists of just such forms, especially among the titanotheres.

Oxyaena was primitively not unlike *Limnocyon verus* in the adaptation of the skull, jaws, and teeth. The lower molars were essentially tuberculo-sectorial and the upper were tritubercular; however, since none of the Upper Paleocene creodonts had truly sectorial carnassials, this does not mean that they were not truly carnivorous. The later species of *Oxyaena* were larger, with a better developed carnassial shear, fairly robust, crushing premolars, strong canines, and heavy jaws. They were well adapted for eating meat and crushing bones.

Patriofelis includes heavy-jawed forms with powerful skulls, well developed shearing molars, and robust, quickly blunted premolars and canines. Among the fissipedes, the nearest analogue is *Hyaena* and it is entirely possible that *Patriofelis* fed on carrion to some extent, but there is no evidence for this hypothesis. Wortman (1894, p. 161) believed that *P. ferox* habitually fed on turtles for the following reasons: (1) he thought *Patriofelis* was aquatic; (2) turtles were abundant in the Bridger beds; (3) coprolites with fragments of turtle bones have been found in the Bridger beds; (4) the powerful jaws and teeth were capable of crushing turtle shells. Although, as will be shown below, there is good reason for believing that *Patriofelis* was not aquatic, there is much to be said for Wortman's theory, since turtles might have been captured in swamps, river borders, or shallow water. Moreover, there is no other carnivorous form known in the Bridger beds which is as well adapted in its feet and teeth for catching and eating turtles. Matthew (1909, p. 432) concluded that *P. ferox* "was probably an indiscriminate and voracious feeder like the modern hyaenas, gluttons, etc." Since this form was a slow, lumbering animal, unable to capture speedy prey, this is a reasonable conclusion; it is a safe assumption that turtles and alligators formed part of its diet. *P. coloradensis* and *P. ulta* are smaller, but probably had a similar diet. *P. compressa*, however, was a much less robust animal, not only in its jaws and teeth, but also in its limbs. It was better adapted for catching and eating some of the contemporary slow-moving herbivores.

Sarkastodon carries the tendencies of *Patriofelis ferox* to an extreme. The teeth in the posterior part of the jaw are of a very specialized meat-shearing type, while the anterior teeth are tremendously robust and rapidly blunted. The skull and jaws are capable of powerful crushing action. The conclusions as to the feeding habits are much the same as for *P. ferox*. Turtles may have formed part of the diet of this animal also, since they occurred plentifully in the Irdin Manha beds.

Palaeonictis and *Ambloctonus* have no close analogues among recent carnivores. The short, heavy skull and jaws, and the robust premolars resemble those of the larger species of *Oxyaena*, but the shearing function of the molars is poorly developed. This, together with the ambulatory gait, may mean that they were rather indiscriminate feeders, such as *Hyaena*, and it is probable that carrion formed a large part of their diet.

Locomotor Adaptation

ARBOREAL: An arboreal type, modified for running on branches, is difficult to distinguish from a terrestrial, ambulatory type by its skeleton alone. Such an animal is characterized especially by: (1) divergent, somewhat opposable pollux and hallux; (2) free power of pronation and supination of the manus; (3) perhaps a prehensile tail; (4) sharp, curved claws; (5) the free and varied movements of the limbs; and, (6) the presence of a clavicle.

(1) The pollux and hallux are divergent to some degree in all the Oxyaenidae. Since this is a heritage character, carried over from ancestors which were certainly arboreal (Matthew, 1904), it is no proof of arboreal habits. The divergence is somewhat less in the Limnocyaninae.

(2) *Thinocyon* and *Oxyaena platypus* are the only broad-skulled Pseudocreodi with a round-oval head on the radius. All the others have a moderately to very wide-oval head, indicating reduced ability to pronate and supinate the hand.

(3) The tail of the Eocene Pseudocreodi was long and strong, but there are no certain criteria by which it can be told whether it was prehensile or not. It may be only an inheritance from arboreal ancestors.

(4) The ungual phalanges of all the Oxyaenidae are short, blunted and flattened dorso-ventrally; they are entirely unadapted for holding onto bark. The claws of the Limnocyoninae are longer and sharper, but are little curved, and are not fitted for climbing.

(5) The depth and width of the cotyloid notch of the pelvis is a single character which gives a reliable indication of the freedom of motion of the hind limb. In most of the Oxyaenidae and in *Limnocyon* it is moderately wide and shallow, but it is more of the type of a terrestrial ambulatory animal such as *Procyon*, rather than being extremely wide and open as in the arboreal *Arctictis*. In *Thinocyon* and *Oxyaena platypus* it is deeper and narrower, indicating more restricted femur movements.

(6) The clavicle was probably present and well developed in all of the early Pseudocreodi. This is another character which was inherited from arboreal ancestors, and has little adaptive significance, at least in the Eocene.

In summary it may be said that there is no good evidence for arboreal habits in any of the broad-skulled Pseudocreodi. In the Oxyaenidae, the short foot, flat, blunt claws, slight ability to pronate and supinate the manus, as well as the reduction of the motility of the back, are all against such an adaptation. Moreover, the Upper Paleocene and Lower Eocene forms occur in beds which include mostly an open country fauna, and have a very small arboreal element. Among the Limnocyoninae, *Thinocyon* is the only form which has the power of pronation and supination well developed. But its feet are subdigitigrade, and the divergence of the hallux is slight; it is most improbable that it is arboreal.

CURSORIAL: None of the broad-skulled Pseudocreodi can be classified as truly cursorial. Carnivora which are fitted for such a manner of locomotion have a digitigrade foot, long, compact carpus, tarsus and metapodials, long forearm and shank, shortened tail, light limbs and body, and exhibit many other highly characteristic adaptations. Only *Thinocyon* and *Oxyaenodon*, and perhaps *Prolimnocyon* and *Thereutherium* approach the cursorial type. The first two have a relatively long, compact foot which is subdigitigrade; the divergence of the pollux and hallux is reduced; the forearm and shank are moderately long; the body and limbs are relatively slender. They might be called subcursorial.

AMBULATORY: This classification includes most of the broad-skulled Pseudocreodi, certainly *Oxyaena*, *Patriofelis*, *Palaeonictis*, and probably *Limnocyon*. All of them have short, spreading, plantigrade feet, short and heavy limb bones, and robust bodies. Numerous other characters indicating this manner of locomotion have been mentioned in the preceding section. The skeleton of *Prolimnocyon* is poorly known, but the pelvis, tibia and calcaneum indicate a moderately light-limbed, ambulatory or subcursorial animal, probably similar to *Sinopa*. The exceedingly broad, spreading feet of *Patriofelis ferox* may be an adaptation for walking on soft ground, perhaps in swamps and on river banks; this accords with the theory that they fed on turtles. The Bridger and Washakie formations, in which it occurs, are made up largely of deposits of streams, swamps, and flood-plains, and adds further support to this hypothesis.

FOSSORIAL: The only member of the Pseudocreodi which shows any indication of digging habits is an undescribed Mongolian form.

AQUATIC: The early stages of aquatic adaptation are difficult to determine from skeletal characters alone. The most obvious skeletal distinction of a truly aquatic carnivore is the shortening of the proximal and lengthening of the distal segments of the limbs. Wortman (1894, p. 161; 1902, p. 127) argued that *Patriofelis* was aquatic, but Matthew (1909, p. 429–431) showed that the short tibia, metapodials and phalanges are specialized in just the opposite way from aquatic carnivores. The same is true to a greater or less degree of all the Oxyaenidae. Among the Limnocyoninae, *Thinocyon* shows a lengthening of the tibia, metapodials and phalanges, but the proportions of the limb-segments resemble those of *Felis* as closely as those of the semi-aquatic *Mustela.* The sharply convex distal articulatory facet of the metapodials, with a distinct fossa above it, indicates a flexible joint between the metapodials and proximal phalanges, with considerable angulation at this joint. This is highly suggestive of a subdigitigrade, subcursorial manner of locomotion. In aquatic forms the flexibility of the joints of the feet is greatly reduced. The forefoot of *Oxyaenodon* is relatively long also, but the lengthening of the forearm and the character of the distal articulatory surface of the metacarpals indicates a subcursorial gait. In summary, there is no evidence that any of the broad-skulled Pseudocreodi were aquatic or even semi-aquatic.

GENERAL RELATIONSHIPS

Relationships of the Limnocyoninae

In 1902 (p. 117) Wortman grouped *Limnocyon, Thinocyon, Oxyaenodon,* and *Thereutherium* in the Limnocyoninae, which he used as a subfamily of the Oxyaenidae, as opposed to the Oxyaeninae. Later authors have followed Wortman in retaining this group within the Oxyaenidae, but many have noted its close resemblance to the Hyaenodontidae, especially to the more primitive Proviverrinae. Matthew in 1905 (p. 72) states that "the relationship of *Sinopa* to the Oxyaenidae, especially to *Limnocyon,* is not yet clear. There is a great deal of resemblance in skeletal characters, a marked diversity in the more significant features of the skull. Most of the resemblance, perhaps all, is to be explained as due to retention of primitive creodont characters, but some may indicate a nearer relationship of Hyaenodonts to Oxyaenids than to any other creodont family. . ." In 1909 (p. 330) and 1915 (p. 71) he is convinced that the Oxyaenidae (including the Limnocyoninae) and Hyaenodontidae are nearly related and unites them in the superfamily Pseudocreodi. Scott in 1913 (p. 573)

believes that the Limnocyoninae "were survivors of still more ancient and primitive progenitors of the family [Oxyaenidae]", and that, "*Limnocyon* . . . tends to indicate a common origin for the oxyaenids and hyaenodonts . . ."

It is the conviction of the author that the similarity between the skeleton of the Limnocyoninae and that of the Proviverrinae is indicative of a very close relationship. On the other hand, the resemblance of the Limnocyoninae and Oxyaenidae is a result of the retention of primitive creodont characters and of the somewhat similar adaptation in both, and is thus due to parallelism. The most important character which the Oxyaeninae and Limnocyoninae have in common is the absence of M$\frac{3}{3}$, and the development of M$\frac{1}{2}$ as the main carnassials. This has been considered by Matthew and others to be a fundamental difference from the typical hyaenodontid condition, in which M$\frac{2}{3}$ are the largest carnassials. But *Sinopa mordax* and *Prolimnocyon*, which have M$\frac{3}{3}$ more or less reduced, are ideal intermediate forms and show how the typical proviverrine could give rise to the oxyaenid arrangement. The proportions of the skull and jaws of the Limnocyoninae are intermediate; the most specialized members of the group closely approach, but never quite attain the proportions found in the earliest oxyaenine. The post-cranial skeleton of the Limnocyoninae is much closer to that of the Proviverrinae than to that of the Oxyaeninae; *Limnocyon* is similar to *Tritemnodon*, while *Thinocyon*, and perhaps *Prolimnocyon* and *Oxyaenodon*, approach *Sinopa* in proportions.

Below is presented a list of some important characters in which the Limnocyoninae resemble the Proviverrinae and differ from the Oxyaeninae:

Limnocyoninae and Proviverrinae	*Oxyaeninae*
P$\frac{1}{1}$ two-rooted, except in some specialized genera.	P$\frac{1}{1}$ single-rooted or absent.
P^3 simple, usually two-rooted, lacking distinct protocone.	P^3 developing protocone early; three-rooted, except in earliest forms.
P^4 and M^1 with moderately short metastyle.	P^4 and M^1 with long metastyle.
Shearing blade of carnassials less perfectly developed.	Shearing blade of carnassials rapidly perfected
Cheek tooth-row relatively long.	Cheek tooth-row moderately to very short
Lower jaw very long and shallow to moderately short and deep.	Lower jaw relatively deeper and shorter.
Symphysis relatively long to fairly short and deep.	Symphysis very short and deep.
Angle of jaw slender, projecting, upcurved and pointed at tip.	Angle of jaw deep, robust, projecting little, bluntly rounded or truncate.
Face relatively long.	Face considerably shortened.
Skull narrow to moderately wide.	Skull wide to very wide.
Preglenoid crest none.	Preglenoid crest present.

Limnocyoninae and Proviverrinae	*Oxyaeninae*
Paroccipital process thin, spatulate, and directed mostly posteriorly.	Paroccipital process more robust and directed more ventrally.
Facial nerve exiting through foramen stylomastoideum primitivum.	Facial nerve exiting more ventrally through foramen stylomastoideum definitivum (*Oxyaena* and *Patriofelis*).
Sacrum with distinct anterior process from lateral mass.	Sacrum with no indication of lateral process.
Manubrium expanding anteriorly and flattened dorso-ventrally.	Manubrium laterally compressed, not expanding much anteriorly.
Deltoid crest of humerus tapering off gradually at middle of shaft.	Deltoid crest of humerus ending abruptly about two thirds of way down shaft.
Dorsal border of ilium moderately expanded.	Dorsal border of ilium very high.
Proximal tibial facet of fibula facing internally and proximally.	Proximal tibial facet of fibula facing nearly directly proximally.
Cnemial crest of tibia ending above middle of shaft with a peculiar emphasis distally.	Cnemial crest of tibia tapering off gradually below middle of shaft.
Feet relatively longer, less robust, and spreading.	Feet shorter, robust, and spreading.
Radial surface of scaphoid unexpanded posteriorly on ulnar side.	Radial surface of scaphoid with a characteristic posterior swelling on lateral side.
Unciform wide, but shallow proximodistally.	Unciform narrower, and deeper proximodistally
Lunar-unciform contact small.	Lunar-unciform contact large.
Body of astragalus moderately deep.	Body of astragalus flat.
Trochlear surface of astragalus extends onto neck and is more extensive proximomesially.	Trochlear surface of astragalus limited to body and shorter at proximo-mesial corner.
Calcaneum with large fibular facet.	Calcaneum with fibular facet small or usually absent.
Cuboid-astragalus contact small.	Cuboid-astragalus contact large.
Ungual phalanges laterally compressed.	Ungual phalanges dorso-ventrally flattened.

Although mere enumeration of characters leads to no certain conclusion, a study of important features of the skeleton indicates that the resemblance to the Proviverrinae is more fundamental, that to the Oxyaeninae more superficial and adaptive. The Limnocyoninae are referred therefore to the Hyaenodontidae, while the Oxyaeninae are retained in the Oxyaenidae. It is believed that this expresses the true relationship of the subfamily more correctly, and it emphasizes the fact that the similarity to the Oxyaenidae is due largely to parallelism.

Origin of the Limnocyoninae

It has been shown above that the Limnocyoninae are very closely allied to the Proviverrinae, and the intermediate forms *Prolimnocyon* and *Sinopa mordax* leave little doubt that the former were derived from the latter. When *Prolimnocyon* first appears in the lower part of the Lower Eocene, it is not far removed structurally from *Sinopa*, and it is a safe conclusion that the divergence of the Limnocyoninae from the Proviverrinae began as late as the Upper Paleocene. The central type of both subfamilies was probably such a form as *Sinopa*.

The more remote ancestry of the Hyaenodontidae is uncertain. The family is unknown in the Paleocene with the possible exception of the Mongolian *Opisthopsalis* and *Sarcodon*. The following groups of creodonts occur in the lower and middle Paleocene:

(1) Miacidae, already showing the typical carnassial specialization of $P^{\underline{4}}$ and $M_{\overline{1}}$, and thus excluded from ancestry to other families of creodonts.

(2) Mesonychidae, exhibiting the characteristically long orbital region, low glenoid with a preglenoid crest, very long jaw with robust symphysis, single-rooted first premolars, reduced $M_{\overline{3}}$, and reduced paraconid. These and other characters show that the Paleocene mesonychids are widely separated from the hyaenodontid line at this early date.

(3) Arctocyonidae, as used by Matthew (1937), including a heterogenous assemblage of primitive creodonts, representing several divergent phyla. The Arctocyoninae are shown to be entirely distinct by their low-crowned, quadritubercular molars. The Triisodontinae parallel the Mesonychidae in skull, jaws and teeth, and are as far removed as the latter from the Hyaenodontidae. The Oxyclaeninae and Chriacinae include somewhat more generalized forms, which resemble the Hyaenodontidae in many respects. But all the known genera are specialized in certain ways which exclude them from direct ancestry. For example, the first premolar is single-rooted or absent; there is often a rudimentary hypocone on the upper molars; the trigonids of the lower molars are low; the paraconids are reduced; $M_{\overline{3}}$ is reduced in the Oxyclaeninae.

In conclusion it may be said that the genus or subfamily which was ancestral to the Hyaenodontidae is unknown, but was not far removed from the Chriacinae or Oxyclaeninae.

Relationships of the Palaeonictinae

Palaeonictis was described by de Blainville as a member of the Viverridae (1842, p. 79). Cope in 1875 (B, p. 446, 447) included *Ambloctonus* and *Palaeonictis* in his newly created suborder of Creodonta, and in 1877 (p. 89) referred them both to a separate family, the Ambloctonidae. Osborn and Wortman in 1892 included these genera in the Palaeonictidae (synonym of Ambloctonidae), which they considered ancestral to the Felidae through "*Aelurotherium.*" In 1909 (p. 410, 411) Matthew showed that the derivation of the Felidae from the Palaeonictidae or "*Aelurotherium*" was impossible, and placed *Palaeonictis* and *Ambloctonus* provisionally in the Oxyaeninae. In

1915 (p. 42), he states that these genera form a separate group, *i.e.*, subfamily, within the Oxyaenidae, but gives it no name. Sinclair and Jepsen described a nearly complete skeleton of *Palaeonictis* in 1929, and concluded (p. 171) that "the skeleton of *Palaeonictis* is typically oxyaenid, and there can be no question of the propriety of placing this genus in the Oxyaenidae rather than in a family of its own."

The conclusions arrived at after the present study are entirely in accord with those of Matthew, and of Sinclair and Jepsen, but the two genera are placed in a separate subfamily, the Palaeonictinae, because of the different specialization of the molars. The Upper Paleocene *Dipsalodon* serves to bridge the gap between the Oxyaeninae and Palaeonictinae in tooth-structure. $M_{\overline{1}}$ and $M_{\overline{2}}$ are subequal and much like those of *Oxyaena platypus*, *O. aequidens* and *Dipsalidictides*. It is only the details of the tooth-construction which indicate that *Dipsalodon* belongs to the Palaeonictinae rather than the Oxyaeninae. So far as known, *Palaeonictis* agrees with the Oxyaeninae in the characters of the skull, jaw, and post-cranial skeleton listed above, and differs correspondingly from the Limnocyoninae.

Origin of the Oxyaenidae

In the upper Paleocene, when the Limnocyoninae had not yet become distinct from the Proviverrinae, the Oxyaenidae already possessed the typical family specializations, and were beginning to diverge along the two subfamily lines. Before that time, no oxyaenid is known. Among the early Paleocene Creodonta, the Triisodontinae resemble and approach the Oxyaenidae in many respects; some of the similarities are listed below. The jaw is relatively deep and robust, especially in *Triisodon*. The chin is steep and the symphysis is large and deep, with a vague indication in *Triisodon* of a division into two lobes posteriorly, as in the Oxyaenidae. The angle of the jaw is much as in the Palaeonictinae. The skull has a relatively wide glenoid with a preglenoid crest, similar to that of *Palaeonictis*. The zygomatic arch is strong, and deepens somewhat posteriorly. The nasals of *Eoconodon* are constricted at the middle, widest at the maxillo-frontal suture, and taper posteriorly. The post-orbital processes and supra-orbital ridges resemble those of the Oxyaenidae. The lower incisors are small and crowded, and in *Eoconodon* $I^{\underline{3}}$ is larger than $I^{\underline{1-2}}$ as in the Oxyaenidae. The canines are fairly robust and similar in form to those of *Palaeonictis* and *Oxyaena*. The first premolars are one-rooted. In *Eoconodon* $P_{\overline{2}}$ is erect and $P_{\overline{3-4}}$ lean posteriorly, exactly as in *Dipsalodon*. The lower premolars are moderately robust. $P_{\overline{4}}$ has a

well developed anterior basal cusp, as in the earliest Palaeonictinae. There are often internal cuspules on the heels of $P_{\overline{3}}$ and $P_{\overline{4}}$, as in *Dipsalodon* and *Palaeonictis*. $M_{\overline{1}-\overline{2}}$ are subequal and $M_{\overline{3}}$ is greatly reduced in *Goniacodon*, less so in *Triisodon*. The trigonids of the lower molars are rather high in *Triisodon*. The talonids of *Goniacodon* resemble those of *Oxyaena* in having simple, indistinct cusps; in *Triisodon* and *Eoconodon* the talonid cusps are large and distinct as in the Palaeonictinae. The Triisodontinae approach the Oxyaenidae in the small size of $M^{\underline{3}}$, and in *Goniacodon* and *Triisodon* in the reduction of $M^{\underline{2}}$, especially at the postero-external corner. The postcranial skeleton resembles that of the early Oxyaenidae very closely. Especially characteristic is the deltoid ridge of the humerus, which is robust and terminates abruptly below the middle of the shaft. The cnemial crest of the tibia is broad and low and tapers off gradually towards the middle of the shaft, as in the Oxyaenidae. The astragalus and calcaneum are very similar in the two groups, and the latter has the fibular facet reduced.

Not all of these similarities are found in any one of the three genera of the Triisodontinae, and several important differences from the Oxyaenidae occur. For example, the paraconid of the lower molars is greatly reduced, except in *Eoconodon*, whereas it is enlarged in the Oxyaenidae. The protoconid and metaconid are usually more connate than in the early Oxyaenidae. The presence of $M\frac{3}{3}$ and the relatively unreduced $M^{\underline{2}}$ are characters which would be expected in the ancestors of the Oxyaenidae. The metastyle of the upper molars is very small; in this respect, the difference is less from the Palaeonictinae. The paracone and metacone are more distinctly separated than in the Oxyaenidae. $P^{\underline{3}}$ is three-rooted with a small but distinct protocone; $P^{\underline{3}}$ of *Triisodon* is not very different from that of *Palaeonictis*, but in the earliest Oxyaeninae it is a simple, two-rooted tooth, without a protocone. Since the protocone is present almost invariably in the Paleocene Creodonta, it is possible that it was lost, and that a new cusp appeared in the Oxyaeninae.

On the whole, it appears that direct derivation of the Oxyaenidae from any known member of the Triisodontinae is impossible. But there are so many points of resemblance between the two groups that it is probable that they had a common and not very remote ancestor. This raises the question of the propriety of the use of the superfamily Pseudocreodi to unite the Oxyaenidae and Hyaenodontidae. Although the parallelism of the Limnocyoninae and Oxyaenidae might be taken to indicate a close relationship, the early Proviverrinae show no

approach to the Triisodontinae. It is possible that certain of Matthew's (1909) superfamily groupings should be revised.

Possibility of Descendants of the Oxyaenidae

Certain authors have been misled by the superficial resemblances of the teeth of *Patriofelis* to those of the Felidae into believing in a relationship between the two groups. Leidy, in describing *Patriofelis ulta*, referred it to the "cat family" (1870, p. 10). Marsh believed *Limnofelis* (synonym of *Patriofelis*) to be allied to the cats (1877, p. 369). Cope believed that the Oxyaenidae gave rise to the Felidae (1880 A, p. 81; 1884 A, p. 264). However, Scott pointed out in 1889 (p. 242) that the analogies between the teeth of cats and oxyaenids were only superficial since they are between teeth which are not homologous. Wortman (in Osborn and Wortman, 1892, p. 101) was unconvinced by Scott's reasoning and concluded that the "Palaeonictidae," including *Palaeonictis, Ambloctonus* and *Patriofelis*, were probably ancestral to the Felidae. Adams (1896, p. 442) referred *Patriofelis "leidyanus"* of Wortman to *Aelurotherium*, which he considered intermediate between *Palaeonictis* and the cats. In 1909 (p. 410 and 419) Matthew thoroughly discussed the problem and concluded that *Aelurotherium* was the milk dentition of *Patriofelis* and hence had $M^{\underline{1}}$ and $M_{\overline{2}}$ as the main carnassials, instead of $P^{\underline{4}}/M_{\overline{1}}$ as in the Felidae; and, that *Palaeonictis* was truly oxyaenid and in no way related to the cats or other fissipedes.

In 1894 (p. 157) Wortman first proposed the theory that *Patriofelis* was ancestral to the seals; he defended this idea in 1899 (p. 146) and in 1902 (p. 128). Scott (1895, p. 720) was sceptical from the first, believing that the gap between the Oxyaenidae and Pinnipedia was too great to arrive at any such conclusion. In 1900 (p. 270) Osborn concluded that the trend of adaptation of the Oxyaenidae was divergent from that of the seals, and that the two were unrelated. Matthew (1909, p. 413–416) carefully analyzed the evidence and concluded that there was little in favor of Wortman's hypothesis. On the contrary, he concluded that the Pinnipedia "are derivable from the Arctoid Fissipedia, with especial affinities to the Ursidae. . ."

It appears, therefore, that the Oxyaenidae died out at the end of the Eocene without leaving any successors.

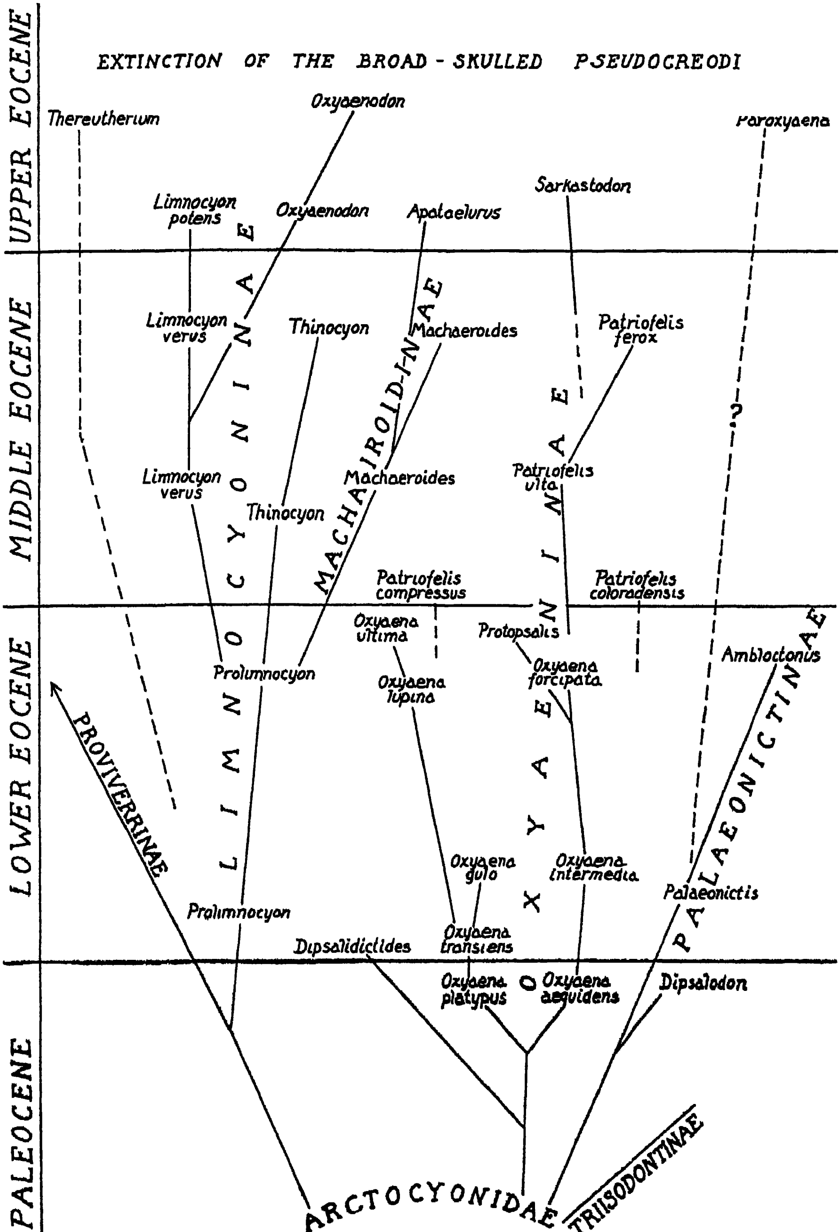


FIGURE 32. Phylogeny of the broad-skulled Pseudocreodi.

PHYLOGENY

The conclusions concerning the relationship and phylogeny of the broad-skulled Pseudocreodi are presented diagramatically in FIGURE 32. In the Oxyaeninae, *Dipsalidictides* is represented as a primitive side line. There are apparently two phyla within the genus *Oxyaena:* (1) large, robust, broad-toothed forms, starting with *O. aequidens* and culminating in *O. forcipata* and *Protopsalis;* (2) relatively small, slender, narrow-toothed animals, beginning with *O. platypus* and ending in *O. lupina* and *O. ultima; O. gulo* is connected with *O. transiens* by intermediate forms, but approaches the *aequidens-forcipata* line in robustness. *Protopsalis tigrinus* is intermediate to *Patriofelis,* but is not considered to be ancestral to any of the species of the latter genus because of its large size. There is a considerable gap between the known species of *Patriofelis* and *Oxyaena. P. compressa* is probably derived from the *O. platypus-O. lupina* phylum because of its slender premolars. *P. ulta* and *P. ferox* are possibly offshoots of the *O. aequidens-O. forcipata* line. The derivation of *P. coloradensis* is uncertain; in its small size, very robust premolars, and relatively small $M_{\overline{3}}$ it is quite distinct from the other species of the genus. The Mongolian *Sarkastodon* is derived from the larger and more robust species of *Patriofelis.*

In the Palaeonictinae, *Dipsalodon* is an ideal ancestral type for *Palaeonictis,* but the known species is probably not the actual ancestor. There is nothing to debar *Palaeonictis* from being the progenitor of *Ambloctonus.*

Prolimnocyon is shown as the central type of the Limnocyoninae, connecting them with the Proviverrinae. From it arose three separate phyla: (1) the cat-like Machaeroidinae; (2) the small, slender-jawed *Thinocyon;* (3) the larger, more robust, deeper-jawed *Limnocyon;* this latter genus may have given rise to *Oxyaenodon.* The European *Thereutherium* is probably the result of a long, separate evolution which took place during the period when North America and Europe were not connected. The ancestral type may have been a primitive limnocyonine, such as *Prolimnocyon,* which could have lived in Europe in the Lower Eocene; or *Thereutherium* may have been derived directly from an early proviverrine, some of which are known in the Lower Eocene of Europe.

BIBLIOGRAPHY

Adams, George Irving.

1896. The extinct Felidae of North Ameria. Amer. Journ. Sci. IV. 1: 419–444. *pl. 10–12.*
[Describes the milk dentition of *Patriofelis* as *Aelurotherium*, which he considers intermediate between *Palaeonictis* and the Felidae.]

Bardenfleth, Knud Stampe.

1913. Notes on the form of the carnassial tooth of carnivorous mammals. (With a critical sketch of the most important tooth-cusp-theories.) Vidensk. Medd. Naturhist. For. Kjöbenhavn 65: 67–111. *figs. 1–15.*
[Follows Winge's cusp nomenclature and classification; refers *Palaeonictis* to Carnivora Vera (107).]

Blainville, Henri Marie Ducrotay de.

1842. Ostéographie ou description iconographique comparée du squelette et du système dentaire des Mammifères récents et fossiles. 2: Secundates. Des Viverras 1–100. *pl. 1–13.*
[Describes and figures *Palaeonictis gigantea* (76–79, *pl. 13*), which he considers a viverrid.]

Cope, Edward Drinker.

1874. Notes on the Eocene and Pliocene lacustrine formations of New Mexico, including descriptions of certain new species of vertebrates. . . Ann. Rep. Chief Eng. 1874: App. FF_3. 591–606.
[Three new species, *Oxyaena lupina*, *O. morsitans*, and *O. forcipata*.]

1875A. Systematic catalogue of Vertebrata of the Eocene of New Mexico. Collected in 1874. 1–37. (Geog. Surv. West 100th Mer.).
[*Ambloctonus sinosus*, new genus and species (8).]

1875B. On the supposed Carnivora of the Eocene of the Rocky Mountains. Proc. Acad. Nat. Sci. Phila. 1875: 444–448.
[First use of the term Creodonta; includes *Amblo**ctonus***, *Oxyaena*, *Stypolophus*, *Didymictis*, *Pterodon* and *Palaeonictis*.]

1877. Report upon the extinct Vertebrata obtained in New Mexico by parties of the expedition of 1874. Geogr. Surv. West 100th Mer. 4 (2): 1–370. *pl. 22–83.*
[Describes and figures *Amblyctonus sinosus*, *Oxyaena morsitans*, *O. lupina*, *O. forcipata*. Discusses general relationships of the Creodonta.]

1880A. On the genera of the Creodonta. Proc. Amer. Phil. Soc. 19: 76–82.
[Relationships, classification, and phylogeny of creodonts.]

1880B. The bad lands of the Wind River and their fauna. Amer. Nat. 14: 745–748.
[*Protopsalis tigrinus*, new genus and species.]

1882. *Mesonyx* and *Oxyaena*. Amer. Nat. 16: 334.
[The foot of *Oxyaena* adapted for swimming.]

1884A. The Vertebrata of the Tertiary formations of the West. Book I. Rep. U. S. Geol. Surv. Terr. 3: i–xxxv & 1–1009. *pl. 1–75a.*
[General discussion of the Creodonta and description of *Oxyaena forcipata* and *Protopsalis tigrinus*.]

1884B. The Creodonta. Amer. Nat. 18: 255–267, 344–353, 478–485. *figs. 1–30.*
[Classification of creodonts and relationship to Carnivora.]

1889. The mechanical causes of the development of the hard parts of the Mammalia. Journ. Morph. **3**: 137–277. *figs. 1–93* + *pl. 9–14*.
[Discussion of revolute zygapophyses (211–213).]

Edinger, Tilly.

1929. Die fossilen Gehirne. Ergeb. Anat. Entwickl. III Abt. **28**: 1–249. *figs. 1–203*.
[Brain of fossil carnivores (150 ff.).]

Filhol, Henri.

1876. Mammifères fossiles nouveaux provenant des dépôts de phosphate de chaux du Quercy. Compt. Rend. Acad. Sci. Paris **82**: 288, 289.
[Original description of *Thereutherium thylacodes*.]

1877. Recherches sur les Phosphorites du Quercy. Ann. Sci. Geol. Paris **8**: 1–340. *pl. 1–28*.
[*Thereutherium thylacodes* described and figured (2–7. *pl. 1, figs. 189–196*).]

1882. Note relative à la présence du genre *Oxyaena* parmi les Mammifères fossiles du Quercy. Bull. Soc. Philomath. Paris VII. **6**: 120, 121.
[Original description of "*Oxyaena*" *galliae*.]

1884. Descriptions de quelques Mammifères fossiles des Phosphorites du Quercy. Ann. Soc. Sci. Phys. Nat. Toulouse **1884**: 1–46. *pl. 1–13*.
["*Oxyaena*" *galliae* described and figured (23–25. *pl. 7*).]

Gervais, François Louis Paul.

1859. Zoologie et paléontologie françaises. Deuxième édition. i–viii + 1–544. *figs. 1–51* + *pl. 1–84*.
[*Palaeonictis gigantea* described and figured (225–226. *fig. 26; pl. 25, figs. 11, 12*).]

Granger, Walter.

1938. A giant oxyaenid from the Upper Eocene of Mongolia. Amer. Mus. Novitates **969**: 1–5. *figs. 1–5*.

Gregory, William King.

1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist. **27**: 1–524. *figs. 1–32*.
[Discusses the relationship of creodonts to Marsupialia, Insectivora, and Fissipedia; concludes *Patriofelis* was not ancestral to seals (313–314).]

Hay, Oliver Perry.

1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bull. U. S. Geol. Surv. **179**: 1–868.
[Classification includes Oxyaeninae in the Hyaenodontidae.]

Jepsen, Glen Lowell.

1930A. Stratigraphy and paleontology of the Paleocene of northeastern Park County, Wyoming. Proc. Amer. Phil. Soc. **69**: 463–528. *figs. 1–4* + *pl. 1–10*.
[Original description of *Dipsalodon matthewi* (524–525. *pl. 10, figs. 8, 9*).]

1930B. New vertebrate fossils from the Lower Eocene of the Bighorn Basin, Wyoming. Proc. Amer. Phil. Soc. 69: 117–131. *pl. 1–4.*
[Original description of *Dipsalidictis amplus* (128. *pl. 4, figs. 1, 2*).]

Klaauw, Cornelis Jacob van der.

1931. On the auditory bulla in some fossil mammals, with a general introduction to this region of the skull. Bull. Amer. Mus. Nat. Hist. 62: 1–352. *figs. 1–18.*
[Numerous references to this region in Creodonts.]

Leche, Wilhelm.

1915. Zur Frage nach der stammesgeschichtlichen Bedeutung des Milchgebisses bei den Säugetieren. II. Zool. Jahrb. Abt. Syst. 38: 275–370. *figs. 1–126.*
[Description of the milk dentition of *Thereutherium* (347–348. *figs. 120–121*) and *Patriofelis* (350).]

Leidy, Joseph.

1869. The extinct mammalian fauna of Dakota and Nebraska. Journ. Acad. Nat. Sci. Phila. II. 7: 1–472. *pl. 1–30.*
[First use of the family name Hyaenodontidae (38).]

1870. Remarks on *Elasmosaurus platyurus* and other fossil vertebrates. Proc. Acad. Nat. Sci. Phila. 1870: 9–11.
[*Patriofelis ulta*, new genus and species (10-11).]

1873. Contributions to the extinct vertebrate fauna of the Western Territories. Rep. U. S. Geol. Surv. Terr. 1: 14–358. *pl. 1–37.*
[*Patriofelis ulta* described and figured (114, 115. *pl. 2, fig. 10*).]

Lydekker, Richard.

1884. Notes on some fossil Carnivora and Rodentia. Geol. Mag. II. Dec. III. 1: 442–445. *figs. 1, 2.*
["*Oxyaena*" *galliae* described and figured (445. *fig. 2*).]

1885. Catalogue of the fossil Mammalia in the British Museum. Part I. i–xxx + 1–268. *figs. 1–33.*
["*Oxyaena*" *galliae* described and figured (35–37. *fig. 3*).]

1904. The ancestry of the Carnivora. Knowledge 1: 61–64. *figs. 1–5.*
[Felidae derived from Palaeonictidae through *Aelurotherium;* marsupials derived from Mesozoic "Creodonts".]

Marsh, Othniel Charles.

1872A. Preliminary description of new Tertiary mammals. Part I. Amer. Journ. Sci. III. 4: 122–128.
[*Limnocyon verus*, new genus and species (126, 127).]

1872B. Preliminary description of new Tertiary mammals. Part II. Amer. Journ. Sci. III. 4: 202–210.
[Descriptions of the following new forms: *Limnofelis ferox, Limnofelis latidens, Limnocyon riparius, Thinocyon velox.*]

1872C. Note on a new genus of carnivores from the Tertiary of Wyoming. Amer. Journ. Sci. III. 4: 406.
[Refers *Limnofelis latidens* to new genus, *Oreocyon.*]

1877. Introduction and succession of vertebrate life in America. Amer. Journ. Sci. III. 14: 337–378.
[Considers "*Limnofelis*" as allied apparently to the cats.]

1899. Note on a Bridger Eocene carnivore. Amer. Journ. Sci. IV. 7: 397.
[Refers *Limnocyon verus* to *Sinopa*, and *L. riparius* to the new genus, *Telmatocyon*.]

Martin, Rudolf.

1906. Revision der obereocaenen und unteroligocaenen Creodonten Europas. Rev. Suisse Zool. 14: 405–600. *pl. 16–19.*
[Describes *Thereutherium* (587–596. *pl. 16, figs. 11, 13*); refers "*Oxyaena*" *galliae* to *Paroxyaena*, new genus.]

Matthew, William Diller.

1899. A provisional classification of the fresh-water Tertiary of the West. Bull. Amer. Mus. Nat. Hist. 12: 19–75.
[*Oxyaenodon dysodus*, new genus and species (49).]

1901. Additional observations on the Creodonta. Bull. Amer. Mus. Nat. Hist. 14: 1–38, *figs. 1–17.*
[Classification and relationships of the Creodonta.]

1904. The arboreal ancestry of the Mammalia. Amer. Nat. 38: 811–818.
[An important theory concerning the ancestral mammal.]

1905. Notes on the osteology of *Sinopa*, a primitive member of the Hyaenodontidae. Proc. Amer. Phil. Soc. 44: 69–72.
[Resemblance of *Sinopa* to the Oxyaenidae indicates near relationship (72).]

1906. The osteology of *Sinopa*, a creodont mammal of the middle Eocene. Proc. U. S. Nat. Mus. 30: 203–233. *figs. 1–20 + pl. 16.*
[A complete description of *Sinopa*, and comparison with other creodonts.]

1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. Mem. Amer. Mus. Nat. Hist. 9: 289–567. *figs. 1–118 + pl. 42–52.*
[An important paper for its descriptions, classification, and discussion of the relationships of creodonts.]

1910. The phylogeny of the Felidae. Bull. Amer. Mus. Nat. Hist. 28: 289–316. *figs. 1–15.*
[*Aelurotherium* not ancestral to the Felidae; describes the adaptation of the Machaerodontinae.]

1915. A revision of the Lower Eocene Wasatch and Wind River faunas. Part I. Order Ferae (Carnivora). Suborder Creodonta. Bull. Amer. Mus. Nat. Hist. 34: 4–103. *figs. 1–87.*
[A systematic revision, with a description of several new forms.]

1937. Paleocene faunas of the San Juan Basin, New Mexico. Trans. Amer. Phil. Soc. II. 30: 1–510. *figs. 1–85 + pl. 1–64.*
[The earliest known creodonts described and illustrated.]

Matthew, William Diller; & Granger, Walter.

1924. New Carnivora from the Tertiary of Mongolia. Amer. Mus. Novitates 104: 1–9. *figs 1–7.*
[Original description of *Didymoconus colgatei* and *D. berkeyi*.]

1925. New creodonts and rodents from the Ardyn Obo formation of Mongolia. Amer. Mus. Novitates 193: 1–7. *figs 1–9.*
[Original description of *Ardynictis furunculus.*]

Orbigny, Alcide Charles Victor Dessalines d'.

1836. Note sur le terrain nouvellement découvert à Meudon. Bull. Soc. Géol. France 7: 280–291. *1 fig.*
[Describes a tooth of "*Loutre*"; this is *Palaeonictis*, and is the first oxyaenid mentioned in the literature.]

Osborn, Henry Fairfield.

1892. *Palaeonictis* in the American lower Eocene. Nature 46: 30.
[Original description of *Palaeonictis occidentalis.*]

1895. Fossil mammals of the Uinta Basin. Expedition of 1894. Bull. Amer. Mus. Nat. Hist. 7: 71–105. *figs. 1–17.*
[Describes a jaw of "? *Hyaenodon*" (78. *fig. 3*), later made the type of *Oxyaenodon dysodus.*]

1897. The Huerfano Lake basin, southern Colorado, and its Wind River and Bridger fauna. Bull. Amer. Mus. Nat. Hist. 9: 247–258.
[Describes *Oxyaena huerfanensis* and *Patriofelis* "*ulta*" = *Patriofelis coloradensis.*]

1900. *Oxyaena* and *Patriofelis* restudied as terrestrial creodonts. Bull. Amer. Mus. Nat. Hist. 13: 269–279. *figs. 1–8 + pl. 18, 19.*
[Maintains that these genera were terrestrial or partly arboreal, and that their feet were digitigrade or subdigitigrade; skeletal restorations of *Oxyaena* and *Patriofelis* (*pl. 18, 19*).]

1909. Cenozoic mammal horizons of western North America; with faunal lists of the Tertiary Mammalia of the West, by W. D. Matthew. Bull. U. S. Geol. Surv. 361: 1–138. *figs. 1–15 + pl. 1–3.*
[Zones and horizons of Tertiary mammals established.]

1910. The age of mammals in Europe, Asia, and North America. i–xvii + 1–635. *figs. 1–220.*
[Restorations of *Oxyaena* (*fig. 44*) and *Patriofelis* (*fig. 65*).]

1912. Craniometry of the Equidae. Mem. Amer. Mus. Nat. Hist. II. 1: 55–100. *figs. 1–17.*
[Gives the system of skull measurements used in this paper.]

Osborn, Henry Fairfield; & Wortman, Jacob Lawson.

1892. Fossil mammals of the Wahsatch and Wind River beds. Collection of 1891. Bull. Amer. Mus. Nat. Hist. 4: 80–147. *figs. 1–18 + pl. 4.*
[Palaeonictidae are believed to be ancestral to the Felidae; the skull and jaws of *Palaeonictis occidentalis* are described (104–106. *pl. 4*).]

Peterson, Olof August.

1919. Report upon the material discovered in the Upper Eocene of the Uinta Basin. Ann. Carn. Mus. 12: 40–168. *figs. 1–19 + pl. 34–47.*
[Describes *Oxyaenodon dysclerus* (42–45. *pl. 34, figs. 1–2*) and *Limnocyon douglassi* = *L. potens* (45–48. *pl. 34 + figs. 11–14*).]

Planté, Raimond Louis Gaston.

1870. Sur les lignites inférieurs de l'argile plastique du bassin parisien. Bull. Soc. Géol. France II. 27: 204–216. *figs. 1, 2 + pl. 1.*
[*Palaeonictis gigantea* from Meudon, France (210).]

Schlosser, Max.

1887. Die Affen, Lemuren, Chiropteren, Insectivoren, Marsupalier, Creodonten und Carnivoren des Europäischen Tertiärs. I. Theil. Beitr. Pal. Öster.-Ungarns 6 (1–2): 1–224. *pl. 1–9.*
[General relationship, classification and phylogeny of the Creodonta; *Thereutherium* described and figured (201–204, *pl. 4, 5*).]

Scott, William Berryman.

1888. On some new and little known creodonts. Journ. Acad. Nat. Sci. Phila. II. 9: 155–185. *pl. 5–7.*
[Describes skeleton of *Protopsalis tigrinus.*]

1889. Notes on the osteology and systematic position of *Dinictis felina* Leidy. Proc. Acad. Nat. Sci. Phila. **1889**: 211–244. *figs. 1–7.*
[Analogies between Oxyaenidae and Felidae superficial (242).]

1892. A revision of the North American Creodonta. Proc. Acad. Nat. Sci. Phila. **1892**: 291–323.
[General relationship and classification of the Creodonta.]

1895. On the Creodonta. Rep. Brit. Assoc. Adv. Sci. 65th meeting 1895: 719, 720.
[Doubts that Pinnipedia were derived from Oxyaenidae (720).]

1913. A history of land mammals in the western hemisphere. New York 1913.
[Restoration of *Patriofelis* (*fig. 282*) and *Oxyaena* (*fig. 284*).]

1937. A remarkable sabretooth-like creodont from the Eocene of Utah. Science II. **85**: 454–455.

M S. A problematical cat-like mandible from the Uinta Eocene, *Apataelurus kayi* gen. et sp. nov. (Will be published shortly in the Annals of the Carnegie Museum.)

Sinclair, William John; & Jepsen, Glen Lowell.

1929. A mounted skeleton of *Palaeonictis.* Proc. Amer. Phil. Soc. **68**: 163–173. *figs. 1–5.*
[Description of the only nearly complete skeleton of a member of this subfamily.]

Teilhard de Chardin. Pierre.

1927. Les Mammifères de l'Éocène inférieur de la Belgique. Mém. Mus. Roy. Hist. Nat. Belg. **36**: 1–33. *figs. 1–29* + *pl. 1–6.*
[On *pl. 5* are figured several teeth which may belong to Pseudocreodi.]

Thorpe, Malcolm Rutherford.

1923. Notes on the Bridger (Eocene) Carnivora. Amer. Journ. Sci. V. **5**: 23–39.
[Descriptive and systematic notes.]

Winge, Adolf Herluf.

1895. Jordfundne og nulevende Rovdyr (Carnivora) fra Lagoa Santa, Minas Geraes, Brasilien. E Museo Lundii 2(4): 1–130. *pl. 1–8.*
[An original classification and phylogeny of Carnivora, based largely on tooth-structure.]

1924. Pattedyr-Slaegter. II. Rodentia, Carnivora, Primates. 1–321.
[Classification much as above; Winge's system of cusp nomenclature applied to creodonts.]

Wood, Horace Elmer 2nd; Seton, Henry; & Hares, Charles Joseph.

1936. New data on the Eocene of the Wind River Basin, Wyoming. Proc. Paleont. Soc. **1935**: 394, 395.
[*Patriofelis* from the Wind River Basin, Middle Eocene.]

Wortman, Jacob Lawson.

1894. Osteology of *Patriofelis*, a Middle Eocene creodont. Bull. Amer. Mus Nat. Hist. **6**: 129–164. *figs. 1–5 + pl. 1.*
[Thorough description of the skeleton of *Patriofelis*; believes it is aquatic and ancestral to the seals.]

1899. Restoration of *Oxyaena lupina* Cope, with descriptions of certain new species of Eocene creodonts. Bull. Amer. Mus. Nat. Hist. **12**: 139–148. *figs. 1–3 + pl. 7.*
[The skeleton described and figured is probably *O. forcipata*; also describes the skull and teeth of *Oxyaenodon* "*dysodus*" = *O. dysclerus*.]

1901–1902. Studies of Eocene Mammalia in the Marsh collection, Peabody Museum. Part I. Carnivora. Amer. Journ. Sci. IV. **11**: 333–348, 437–450; **12**: 143–154, 193–206, 281–296, 377–382, 421–432. 1901. **13**: 39–46, 115–128, 197–206, 433–448; **14**: 17–23. 1902.
[Description, classification, revision, and relationships of the Middle Eocene carnivores; an important paper.]

INDEX

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES
VOLUME XXXVII, PAGES 257–272
JUNE, 1938

EFFECT OF NERVE-EXCITATION ON POTASSIUM IN BODY-FLUIDS*

BY RAYMUND LULL ZWEMER AND FRANK HENRY PIKE

CONTENTS

INTRODUCTION

Von Monakow (1914) showed the confusion in the field included under the general term of shock and thereby made clear the necessity of knowing the conditions under which any particular form of shock arose. Potassium elevation to toxic levels has been found to follow extensive tissue-destruction or loss of extracellular body-fluids concomitant with so-called clinical or surgical shock (Zwemer & Scudder, 1937), and it was of interest to determine whether a rise in plasma potassium was common to other types of shock. Neurogenic shock and the peculiar relationships of nerve-excitation to the condition of shock (Meek, 1936; Taylor *et al.*, 1933) led us to investigate changes in the potassium content of body-fluids following excitation of nerves.

* Awarded an A. Cressy Morrison Prize in Natural Science in 1937 by the New York Academy of Sciences. Publication made possible through a grant from the income of the Centennial Fund.

EXPERIMENTAL PROCEDURES

Excitation of nerves was induced in seventeen cats. In five, repeated convulsions followed intravenous injection of camphor-monobromide into the femoral vein under local anesthesia. Another five evinced marked generalized sympathetic discharges following temporary cerebral anemia induced by ligation of the carotid and vertebral arteries under continuous moderate ether anesthesia up to the time of the first occlusion of the head arteries. Electrical intermittent stimulation of the left splanchnic nerves was used in seven cases. One of these was under nembutal anesthesia, the remaining ones under ether. Stimulation for five minutes was followed by a rest of five minutes or more.

More than 200 samples of blood and other body-fluids were obtained before, during, and at the end of the experiments, and analyzed for their potassium-content by the Truszkowski-Zwemer (1937) method, using 0.5 ml. of fluid for duplicate analyses. All the samples from one animal were analyzed together, with six standards of three different concentrations.

RESULTS

The experimental results indicate that a definite increase in serum potassium occurs after excitation of intact nerves. If the stimulus is continued, the rise in potassium may reach toxic levels and the animal dies. The implications of this statement are so far-reaching that we have checked our findings in a number of ways. The initial (Table 1) and post-experimental (Table 2) values are given for all animals, and sample protocols for each of the three types of experiment.

A mass-discharge of nerve impulses accompanied by generalized convulsions has been found to be induced by intravenous injection of absinthe (Pike *et al.*, 1929) or camphor-monobromide (Coombs, Pike, & Searle, 1935). The latter was selected as the stimulating agent for five of the cats (nos. 3714, 3715, 3716, 3719, 3720). In all of them there were marked increases in serum potassium and in four the terminal cerebrospinal fluid had a high potassium-content. Due to excessive muscular activity it was thought that potassium released from skeletal muscle might be largely responsible for the rise, although our multiple blood sampling gave evidence that blood coming from muscle remained more constant than other venous blood.

Cerebral anemia was next used as the exciting agent, since the chief effect of temporary occlusion of arteries to the brain is an easily ob-

served mass discharge of the thoraco-lumbar division of the autonomic nervous system (Stewart *et al.*, 1906; Yates, 1921; Winkin, 1922). The initial blood samples for potassium analysis were taken *after* the operation for isolating the carotid and vertebral arteries so that any effect of tissue damage might be ruled out as contributing to the rise in potassium. In these cases it proved to be an unnecessary precaution, as the analyses showed normal values. Previous experience had intimated (Zwemer & Scudder, 1937) that considerable tissue-damage and fluid-loss are necessary to affect plasma-potassium values. In the series subjected to asphyxia of the brain (Cats 3725, 3726, 3727, 3728, and 3731), the peripheral arterial and venous sera had an increased potassium-content, but this increase was not nearly as striking as that in the portal vein. Furthermore, contrary to experiments reported by others, the living liver appeared to be removing potassium from the blood rather than liberating it. The cerebrospinal fluid also had a potassium-content higher than that of arterial serum taken simultaneously. The experiments of Dulière (1931) and our analyses indicate that the potassium-content of normal cerebrospinal fluid of man and other mammals is definitely lower than that of the normal range of arterial plasma.

The localized increases in potassium were further checked by electrical stimulation of the splanchnic nerves. Five animals with intact splanchnics showed increases in potassium-content of body-fluids after stimulation, as did one in which the distal side of the ligated left splanchnics was stimulated.

In three of these (Cats 3733, 3740, 3742), repeated stimulation of intact splanchnics invoked a collapse which proved fatal; in a fourth (Cat 3735), ligation of the adrenal vessels previous to stimulation reduced the number of stimulation periods necessary to produce collapse.

Under nembutal anesthesia one animal showed no signs of collapse after two hours of stimulation, but an increase in portal blood and cerebrospinal fluid potassium was beginning to appear. The greater difficulty in producing shock under barbiturate anesthetics than with ether or local anesthesia will be referred to in the discussion.

Stimulation of the side distal to a ligature on the splanchnic nerves gave a significant increase of potassium in portal vein blood only (Cat 3739). Three samplings showed that a 30% elevation was maintained for the period of stimulation. Hepatic vein blood taken simultaneously had a potassium-content 50% lower than portal blood

and this did not increase even after twelve periods of stimulation. When the stimulus was shifted to the sciatic nerve, the portal serum potassium returned to the initial level. These observations indicate that the operative procedure, anesthesia, and blood-sampling are not severe enough to be responsible for the observed potassium increases.

When the stimulus was applied to the nerve on the side central to the ligature (Cat 3741), a slight decrease in body-fluid potassium occurred after five periods of stimulation. This returned to the initial level after ten periods.

Further studies are being made of many of the points briefly mentioned here; it seems definite, however, that excitation of intact nerves results in a rise of potassium in body-fluids which may reach lethal levels. With sympathetic stimulation the greatest release is from the regions drained by the portal vein. That the intestine contributes potassium after stimulation is shown by repeated samples from mesenteric veins. The hepatic-portal vein differences constitute strong evidence that the liver *removes* potassium from portal blood and does not *contribute* potassium after splanchnic stimulation.

DISCUSSION

An increase of potassium after nerve-excitation is not a new finding, but the production of a continued release of potassium to exhaustion of the potassium-regulating mechanisms and eventual collapse of the individual has not to our knowledge been reported. Neurogenic shock has however been a common experience of mankind, especially during medieval torture, when it required great finesse to produce maximal nerve excitation while remaining just short of producing collapse. The work of Taylor *et al.* (1933), Meek (1936), and Herrin & Meek (1933) shows the importance of an intact nervous system in the production of shock by various procedures. The fact that the type of anesthesia alters the conditions necessary to produce shock (Seeley *et al.*, 1936) also suggests involvement of the nervous system, and Pichler (1934) reports that the potassium recoverable from the brain after an anesthetic differs from normal.

The observation by Howell (1906, 1908) that liberation of potassium ions occurred after vagus stimulation of the heart has been confirmed by Lehnartz (1936), and there are other papers which suggest that potassium is released after nerve-excitation (Cowan, 1934; Vogt, 1936; Houssay *et al.*, 1937). The effects of carefully controlled elevations in potassium-content of the fluid medium on nerve-conduction (Lehmann, 1937) resemble those of lowered pH.

The effects of an increased potassium-content of the tissue-fluids on cell-activity and well-being are common knowledge, and it should be remembered that an intravenous injection of potassium is about 100 times as toxic as the same amount by mouth. Potassium released endogenously soon reaches the blood-stream, to be carried to all cells unless the amount is effectively reduced on passage through the various capillary beds. The removal of potassium from the blood-stream by the kidney is an accepted fact; the work of Fenn (1936) indicates that skeletal muscle loses and gains potassium with work and recovery. The liver has been reported to release potassium after administration of adrenaline (D'Silva, 1933–1936; Marenzi & Gerschman, 1937) and in the present experiments to store potassium on the evidence of differences in potassium content of hepatic and portal blood. The analyses of bile suggest that some of the potassium removed leaves the liver by that route. Our disagreement with Houssay *et al.* (1937) on the source of potassium released by splanchnic stimulation may be due to the bloods sampled, as their paper does not mention the portal blood potassium-content. Unless one believes that the increased portal blood potassium comes from the stimulated nerves, which is doubtful, it would seem that smooth muscle and other intestinal cells lose potassium after excitation of their nerves. It appears that potassium metabolism differs throughout the body and cell-activity determines its plasma-level in the various veins.

It seems clear, from the evidence now available, that both potassium and calcium (Coombs *et al.*, 1934, 1935) are released into the blood-stream during or following generalized convulsions. In an animal in whose blood ionized calcium is low (as after parathyroidectomy), or when the concentration of potassium in the blood is high (Ingle *et al.*, 1937) (as after bilateral adrenalectomy), the muscle can do but little work before complete fatigue comes on. It might be inferred that a low concentration of calcium in the blood limits the performance of muscle; the fact that intravenous injection of calcium gluconate greatly improves the performances of the muscles tends to substantiate this inference. In the case of potassium, the poor performance of the muscles in the presence of a higher concentration in the blood is open to two interpretations: (1) The presence of so much potassium in the blood interferes with the proper functioning of the muscle; or (2) The high concentration of potassium in the blood indicates that the muscle has lost so much potassium that it can no longer carry on. One is tempted to adopt the first alternative, perhaps

largely because of the traditional view that the accumulation of end-products of metabolism is responsible for the onset of fatigue. But the view that muscles, and probably also nerves, fail because of loss of potassium must be admitted as a possibility. Complicated processes of synthesis are necessary to put the muscular and nervous systems back into condition for further work. From the facts now available on the parathyroid and adrenal, it would appear that some product of one or the other gland may be necessary for getting the calcium or potassium back into chemical combinations in muscle, nerve and other cells. In the absence of these products, loss of calcium and potassium attendant upon ordinary activity is not made good by recombination, and earlier exhaustion is the result.

There is an increasing amount of evidence to indicate that the adrenal cortex is associated with the ability of the body to regulate potassium. Adrenalectomized animals and patients with Addison's disease are more susceptible than normal to potassium by mouth or by injection (Zwemer & Truszkowski 1936, 1937; Allers *et al.*, 1936; Wilder *et al.*, 1936). Animals without adrenals succumb more easily than normals after conditions favoring potassium release (*e.g.*, nerve excitation: Coombs, 1925). The administration of adrenal cortex extract protects against potassium, and its use has been found to be beneficial in conditions in which disturbances of potassium metabolism occur.

Mammalian life is dependent on certain variables (Pike, 1935) of environment, the hereditary physico-chemical basis of the organism, and its endocrine and nervous systems. These are interdependent and changes affecting one may profoundly affect the others. The experiments on potassium distribution after nerve-excitations uggest one way in which the activity of the nervous system may profoundly affect the physico-chemical basis, either directly or indirectly through the endocrine system.

We wish to thank Dr. John Scudder, Mr. H. Hoberman, Miss M. Norkus, Miss M. Sargent and Mrs. H. Konheim for their assistance.

SUMMARY

1. Excitation of the nervous system initiates a release of potassium from cells, which if long continued overcomes the potassium-regulating mechanism and potassium rises to detrimental levels in the body-fluids.

2. Mass-excitation by camphor-monobromide involved both somatic

and visceral nervous systems; temporary cerebral anemia excited preponderantly the whole autonomic system.

3. Electrical stimulation of the splanchnic nerves elicited a local potassium increase in portal blood. The potassium level of the latter was at first reduced on passage through the liver, but with continued stimulation this barrier no longer prevented a general rise of potassium in body-fluids.

4. The experiments reported suggest the need for further detailed studies on potassium metabolism and its control in various nervous disorders.

BIBLIOGRAPHY

Allers, William Duane; Nilson, Hugo Waldemar; & Kendall, Edward Calvin.
Studies on adrenalectomized dogs: the toxic action of potassium. Proc. Staff Mayo Clinic 11: 283–288. 29 Ap 1936.

Coombs, Helen Copeland.
The response to occlusion of the head arteries after adrenalectomy. Am. Jour. Physiol. 72: 200, 201. 1 Mr 1925.

Coombs, Helen Copeland; Pike, Frank Henry; & Searle, Donald Stratton.
The relation of contracture and tetany to experimentally produced calcium deficiency in cats, with and without lesions of the cortical motor areas. Endocrinology 19: 421–431. Jl 1935.

Coombs, Helen Copeland; Searle, Donald Stratton; & Pike, Frank Henry.
The changes in the concentration of inorganic calcium and phosphorus during convulsions of experimental origin, in cats, before and after thyroparathyroidectomy, with and with out bromide therapy. Am. Jour. Psychiatry 13: 761–797. *pl. 2.* Ja 1934.

Cowan, Stuart Lawson.
The action of potassium and other ions on the injury potential and action current in Maia nerve. Proc. Roy. Soc. Lond. B115: 216–260. 2 Je 1934.

D'Silva, John Leonard.
The influence of adrenaline on the blood potassium. Jour. Physiol. 80: 7 P. 9 N 1933.
The action of adrenaline on serum potassium. Jour. Physiol. 82: 393–398. 12 N 1934.
The action of adrenaline on serum potassium. Jour. Physiol. 86: 219–228. 8 F 1936.
Action of adrenaline on the perfused liver. Jour. Physiol. 87: 181–188. 21 Jl 1936.

Dulière, W. L.
Données expérimentales sur la répartition du potassium dans le sang extravasé; comparaison entre la concentration physiologique dans le plasma et la concentration dans le liquide céphalorachidien. Compt. Rend. Soc. Biol. 108: 416–418. 23 O 1931.

Fenn, Wallace Osgood.
Electrolyte changes in rat muscle during stimulation. Am. Jour. Physiol. 116: 47, 48. 1 Je 1936.

Fenn, Wallace Osgood; Cobb, Doris M.
Electrolyte changes in muscle during activity. Am. Jour. Physiol. 115: 345–356. 1 Ap 1936.

Herrin, Raymond Clyde; & Meek, Walter Joseph.
Distention as a factor in intestinal obstruction. Arch. Int. Med. 51: 152–168. Ja 1933.

Houssay, Bernardo Alberto; Marenzi, A. D.; Gerschman, R.
Potassium sanguin et mécanisme sympathique-adrénalino-hépatique. Compt. Rend. Soc. Biol. 124: 383, 384. 4 F 1937.

Howell, William Henry.
Vagus inhibition of the heart in its relation to the inorganic salts of the blood. Am. Jour. Physiol. 15: 280–294. 1 F 1906.

Howell, William Henry; & Duke, William Waddell.
The effect of vagus inhibition on the output of potassium from the heart. Am. Jour. Physiol. 21: 51–63. 1 F 1908.

Ingle, Dwight Joyce; Nilson, Hugo Waldemar; & Kendall, Edward Calvin.
The effect of cortin on the concentrations of some constituents of the blood of adrenal-ectomized rats. Am. Jour. Physiol. 118: 302–308. 1 F 1937.

Lehmann, Jorgen Erik.
The effect of changes in pH on the action of mammalian A nerve fibers. Am. Jour. Physiol. 118: 600–612. 1 Mr 1937.
The effect of changes in the potassium-calcium balance on the action of mammalian A nerve fibers. Am. Jour. Physiol. 118: 613–619. 1 Mr 1937.
The effect of asphyxia on mammalian nerve-fibers. Am. Jour. Physiol. 119: 111–120. 1 My 1937.

Lehnartz, Emil.
Potassium ions and vagus inhibition. Jour. Physiol. 86: 37 P, 38 P. 9 Mr 1936.

Marenzi, A. D.; Gerschman, R.
Adrénaline et potassium sanguin. Compt. Rend. Soc. Biol. 124: 382. 4 F 1937.

Meek, Walter Joseph.
Present day conception of shock. Northwest Med. 35: 325–334. S 1936.

Monakow, Constantin von.
Die verschiedenen Formen des Shocks. In his: Die Lokalisation im Grosshirn. 20–34. *pl. 1.* 18 Ap 1914.

Pichler, E.
Zustandsformen des Kalium im Zentralnervensystem und ihre Abhängigkeit von dessen Erregungslage. Arch. Exp. Path. Pharm. 175: 85–91. 12 Mr 1934.

Pike, Frank Henry.
A naturalistic definition of life. Anat. Rec. 64: Suppl. 1: 94. 25 D 1935.

Pike, Frank Henry; Elsberg, Charles Albert; McCulloch, Warren Sturgis; & Rizzolo, Attilio.
Some observations on experimentally produced convulsions. The localization of the motor mechanisms from which the typical clonic movements of epilepsy arrive. Am. Jour. Psychiatry 9: 259–283. "S" [O] 1929.

Seeley, Samuel Foster; Essex, Hiram Eli; & Mann, Frank Charles.
Comparative studies on traumatic shock under ether and under sodium amytal anesthesia. Ann. Surg. 104: 332–338. S 1936.

Stewart, George Neil; Guthrie, Charles Claude; Burns, Rush Leslie; & Pike, Frank Henry.
The resuscitation of the central nervous system of mammals. Jour. Exp. Med. 8: 289–321. 26 Mr 1906.

Taylor, Norman Burke; Weld, Charles Beecher; & Harrison, George Gerald Kent.
Experimental intestinal obstruction. Canad. Med. Assoc. Jour. II. 29: 227–236. S 1933.

Truszkowski, Richard; & Zwemer, Raymund Lull.
Determination of blood potassium. Biochem. Jour. 31: 229–233. F 1937.

Vogt, Marthe.
Potassium changes in the stimulated superior cervical ganglion. Jour Physiol. 86: 258–263. 9 Mr 1936.

Wilder, Russell Morse; Snell, Albert Markley; Kepler, Edwin John; Rynearson, Edward Harper; Adams, Mildred; & Kendall, Edward Calvin.
Control of Addison's disease with a diet restricted in potassium: a clinical study. Proc. Staff Mayo Clinic 11: 273–283. 29 Ap 1936.

Winkin, Cora (Senner).
An analysis of the nervous control of the cardiovascular changes during occlusion of the head arteries in cats. Am. Jour. Physiol. 60: 1–47. 1 Mr 1922.

Yates, Anna Baker.
The mechanism of the recovery or maintenance of systemic blood pressure after complete transection of the spinal cord. Am. Jour. Physiol. 57: 68–94. 1 Au 1921.

Zwemer, Raymund Lull; Scudder, John.
Potassium changes in experimental shock. Am. Jour. Physiol. 119: 427. 1 Je 1937.

Zwemer, Raymund Lull; Truszkowski, Richard.
Potassium: a basal factor in the syndrome of corticoadrenal insufficiency. Science II. 83: 558–560. 5 Je 1936.
Factors affecting human potassium tolerance. Proc. Soc. Exp. Biol. Med. 35: 424–426. "D 1936" [Ja 1937].
The importance of corticoadrenal regulation of potassium metabolism. Endocrinology 21:40–49. Ja 1937.

TABLE 1

BEFORE EXCITATION OF NERVES

Potassium in mg. per 100 ml. of fluid

Cat No.	Arterial serum	*Venous sera from* Muscle	Brain or Liver	Gut	Cerebrospinal Fluid	Types of Experiment
3714	11.0	15.8	–	–	–	Intravenous camphor-monobromide injections using local anesthesia
3715	13.8	18.9	–	–	–	
3716	17.2	20.4	–	–	–	
3719	19.8	24.6	–	–	–	
3720	19.8	22.5	16.8L	–	–	
3725	17.7	–	15.1B	20.5	–	Cerebral anemia by by occlusion of carotid and vertebral arteries
3726	13.0	12.0	–	18.3	–	
3727	19.9	–	24.3B	–	–	
3728	15.4	–	16.8B	–	–	
3731	–	16.0	–	19.9	–	
3733	–	–	–	20.6	–	Stimulation of intact left splanchnic under ether
3740	11.6	14.6	–	16.9	10.5	
3742	17.5	21.9	15.9L	18.7	–	
3738	23.1	27.4	26.1L	26.2	13.2	Same with nembutal.
3735	–	–	–	26.0	–	Adrenals tied off.
3739	13.9	–	17.0L	24.8	13.7	Distal splanchnic stimulation
3741	19.7	22.2	–	15.4	16.3	Central splanchnic stimulation

Many of these initial values were maintained during the early stages of the procedure.

TABLE 2

AFTER EXCITATION OF NERVES

Potassium in mg. per 100 ml. of fluid

Cat No.	Arterial serum	*Venous sera from* Muscle	Brain	Liver	Gut	Bile	Cerebro-spinal fluid	Number of samples analyzed
3714	28.4	31.1	33.9	–	39.3	–	13.2	9
3715	27.1	23.6	24.0	–	35.5	–	53.8	9
3716	22.7	–	25.1	–	66.3	–	32.9	11
3719	23.6	29.1	19.8	–	37.3	–	32.9	13
3820*	29.1	–	48.1	69.4	92.6	–	39.1	13
3725	26.8	–	23.1	–	33.9	–	34.7	11
3726	22.2	–	24.3	–	23.6	–	22.2	15
3727	32.8	–	–	36.0	51.6	24.0	45.8	14
3728*	–	55.2	–	64.8	139.5	54.0	65.2	13
3731	–	23.1	23.9	23.3	30.8	89.5	33.6	13
3733*	39.8	44.2	–	31.1	33.3	36.0	36.0	19
3740	–	–	–	69.4	–	20.8	38.3	16
3742	29.6	35.9	–	40.2	49.5	33.2	17.5	19
3738	23.2	25.6 –	–	30.4	36.0	38.0	18.3	19
3735	–	–	–	34.0	28.1	34.5	26.3	14
3739	14.9	–	–	14.3	32.4	–	12.4	14
3741	21.8	–	15.7	16.3	17.2	–	16.3	15

* These are terminal values. In some of the other cases a fall in certain of the values occurred on cessation of the stimulus.

TABLE 3

CAMPHOR-MONOBROMIDE INJECTIONS

Potassium in mg. per 100 ml. of fluid

Cat 3715 March 24, 1937. Male; weight 7 lbs.

A. M.	
10:20	Animal fastened on board and novocaine injected into both hind legs, which were then prepared, one for injection and the other for blood sampling.
10:40	Blood-samples. Femoral artery 13.8 mg., femoral vein 18.9.
10:44	I. First injection of 0.2 ml. of 10% camphor-monobromide. Followed by a typical convulsion.
11:11	II. Another 0.2 ml. injection. A little excitement and occasional twitches, but no convulsion.
11:25	III. The injection was increased to 0.27 ml. and a severe convulsion with respiratory effects appeared.
11:30	Blood-samples taken; blood-pressure low. Femoral artery 31.0; femoral vein 21.1.
11:32 11:34	Two very severe convulsions followed each other at these times, so no injection was given.
11:55	The blood-pressure is improving, but sympathetic stimulation is still evident.
P. M.	
12:02	Blood taken. Femoral artery 27.1; femoral vein 23.6.
12:05	IV. Another injection of 0.27 ml. camphor; killed the animal.
12:06	Additional blood-samples taken at once showed portal blood 35.5; jugular 24.0; cerebrospinal fluid 53.8.

TABLE 4

TEMPORARY CEREBRAL ANEMIA

Potassium in mg. per 100 ml. of fluid

Cat 3727 June 2, 1937.

A. M.	
10:30–11:30	Animal anesthetized with ether, and carotids and vertebrals isolated preparatory to ligation. Femoral artery prepared for blood sampling.
11:35	Blood taken. Femoral artery 19.9; jugular vein 24.3.
11:40–11:45	Incomplete asphyxia as a small anomalous vertebral was overlooked.
11:59–12:01 P. M.	Complete asphyxia with rapid respiration then gradual failure; heart developed slow, full beat then rapidly accelerated; pupils dilated widely. Ether off.
12:05	Samples of blood. Femoral artery 23.1; jugular vein 24.0.
12:17	Blood taken again. Femoral artery 22.0; jugular vein 23.0.
12:22–12:24	Another complete asphyxia of brain with typical symptoms; no ether necessary.
12:25	Blood-samples. Femoral artery 24.6; jugular vein.
12:36	Cat resembled a spinal animal, so abdomen was opened for additional samples. Arterial 32.8; hepatic vein 36.0; portal vein 51.6; lymph 20.1; bile 24.0; cerebrospinal fluid 45.8.

TABLE 5

ELECTRICAL STIMULATION OF INTACT SPLANCHNICS

Potassium in mg. per 100 ml. of fluid

Cat 3742 October 12th, 1937.

A. M.	
10:15	Ether anesthesia; exposure of femoral vessels and mid-abdominal incision.
10:30	Initial blood-samples taken for analysis of serum K. Femoral artery 17.5; femoral vein 21.9; hepatic vein 15.9; portal vein 18.7.
10:45	Left splanchnics exposed for stimulation.
10:51–10:56	I. Splanchnics stimulated with platinum electrodes from Harvard coil with 1.5 volts in primary and secondary fixed at 10 cm. Pupils widely dilated at first, then narrowed down and eyes rolled downward showing sclera; slow vertical mystagmus; respirations shallow and rapid.
10:57	Ether-supply increased, as animal is restless.
11:05–11:10	II. Splanchnic stimulation.
11:11	Ether-supply reduced as cat is quiet.
11:17–11:22	III. Nerve stimulated again.
11:30–11:35	IV. Fourth period of stimulation. External strabismus; pupils dilated; cornea pitted; respirations labored.
11:42–11:47	V. Stimulation of splanchnics. During this period the cat was given no ether, as it needed none.
11:50	Blood-samples taken. Femoral artery 21.9; femoral vein 20.5; hepatic vein 20.4; portal vein 20.2.
11:55–12:15	No stimulation and cat allowed to partially recover.
P. M.	
12:16	Blood-samples showed: femoral artery 19.1; femoral vein 20.9; hepatic vein 18.6; portal vein 19.3.
12:20–12:25	VI. Splanchnic stimulation at 10 cm.
12:32–12:37	VII. Splanchnic stimulation at 10 cm. Corneal reflex lost.
12:46–12:52	VIII. Splanchnic stimulation. Heart-beat slow and blood-pressure low.
12:57–1:02	IX. Splanchnic stimulation. Running motion of fore legs.
1:10–1:15	X. During this period of stimulation the first gasps appeared.
1:17	Blood taken while heart still beating, but no femoral blood available. Aorta 29.6; inferior vena cava 35.9; hepatic vein 40.2; portal vein 49.5; bile 33.2; cerebrospinal fluid 17.5.

TABLE 6

EFFERENT SPLANCHNIC STIMULATION

Potassium in mg. per 100 ml. of fluid

Cat 3739	August 25, 1937.
A. M.	
10:30	Ether anesthesia; tracheal tube inserted; blood vessels exposed for sampling.
10:55	Blood taken. Mesenteric artery 13.9; hepatic vein 17.0; portal vein 24.8; cerebrospinal fluid 13.7.
11:10	Splanchnic nerves on left side isolated and a tight ligature placed around them.
11:19–11:24	I. Distal splanchnics stimulated with Harvard coil having 1.5 volts in primary and secondary set at 10 cm. Deep noisy breathing and swallowing actions were the only observable effects.
11:29–11:34	II. Stimulation. Full strong heart-beat; deep respirations.
11:40–11:45	III. Stimulation.
11:46	Blood-samples. Hepatic vein 16.8; portal vein 32.6.
11:50–11:55	IV. During this period the pupils dilated and the nictitating membrane . was obvious.
P. M.	
12:00–12:05	V. Splanchnics stimulated.
12:14–12:19	VI. Splanchnics stimulated.
12:20	Blood-samples taken. Hepatic vein 13.9; portal vein 32.0.
12:26–12:31	VII. Period of stimulation.
12:39–12:44	VIII. Period of stimulation.
12:50–12:55	IX. Breathing very deep and slow during stimulation.
1:00–1:05	X. Splanchnic stimulations (all distal to ligature).
1:15–1:20	XI. Splanchnic stimulations.
1:25–1:30	XII. Splanchnic stimulations.
1:35–1:40	Blood-samples taken; animal in good condition. Arterial 14.9; hepatic 14.3; portal 32.4; cerebrospinal fluid 12.4.
1:40–2:05	During this period the intact sciatic nerves were stimulated, but the splanchnic nerves were not. Unfortunately no somatic blood was taken after this period.
2:05	Samples taken of portal blood 25.0 and cerebrospinal fluid 12.3.

INDEX

Annals of the New York Academy of Sciences
Volume XXXVII, pages 273–328
July, 1938

MORPHOLOGY, BIONOMICS, AND TAXONOMY OF THE CESTODE DIPYLIDIUM CANINUM*

By Carl Ernest Venard

CONTENTS

* A contribution from the Biological Laboratory, University College, New York University. Publication made possible through a grant from the income of the Audubon Fund.

INTRODUCTION

The tapeworm *Dipylidium caninum* (L.), a common parasite of dogs and cats, is cosmopolitan in distribution and has been known since ancient times. A review of surveys on the distribution of this worm in the United States reveals the fact that it infects more than fifty per cent of the dogs, infections ranging up to more than a thousand mature specimens in a single host. These data correspond closely with the results of similar investigations made in other countries. This tapeworm has been reported from several hosts other than dogs and cats. Several instances of its presence in man, or recovery from man, appear in the literature each year, so it is known to be a human parasite of wide geographic distribution. Wild carnivores, related to the domestic dog and cat, have also been reported as hosts.

This tapeworm normally inhabits the small intestine, but it may be found in the large intestine. It is most commonly present in the jejunum. In dogs with heavy infections, the parasite may occur from the opening of the larger pancreatic duct in the duodenum to a region within a few inches of the caecum. Immature specimens are often located in the ileum. The early stages of *D. caninum* develop in the dog flea and in the mallophagan dog louse.

The present study was begun in 1931. At that time it was found impossible to refer specimens of *Dipylidium*, collected from American dogs, to any of the species recently described in this genus. Each worm showed variations in size and position of structures previously used as criteria for the establishment of new species. During a preliminary investigation, the degree of individual variation was studied in living worms and in the same worms after fixation. The normal variation appeared to be very large in the case of *Dipylidium*, and data which had been used for specific diagnosis were obviously of doubtful value. In order to determine the amount and kind of individual variation, it is desirable to compare closely related individuals. To accomplish this aim, tapeworms reared from the eggs of a single proglottid should be studied and the amount of variation determined, and the entire life history of the tapeworm must be completed under controlled laboratory conditions. This has been done, and at the same time the developmental stages have been studied.

The writer wishes to express his indebtedness to Dr. H. W. Stunkard, who has directed this investigation. Dr. R. E. Rebrassier aided in

preliminary studies by providing facilities at The Ohio State University College of Veterinary Medicine. The interest shown by Dr. R. C. Osburn during the time the problem evolved is gratefully acknowledged.

HISTORICAL REVIEW

Adult Dipylidium caninum

The adult tapeworm was undoubtedly known to the ancients. Even the Babylonians had animal doctors to care for their pets, and it is not likely that this parasite escaped their attention. The species was named by Linnaeus in 1758. The genus *Dipylidium* Leuckart (1863), was erected with *D. caninum* as the type species. Previous to the year 1863, *D. caninum* had been placed in several genera, and it has accumulated a long list of names of specific and varietal rank.

The genus *Dipylidium* belongs in the subfamily *Dipylidiinae* Stiles (1896); the limits of the subfamily have been redefined by various authors since that date. At one time (Ransom, 1909) twenty genera were allocated to it. Witenberg (1932), in a revision of the subfamily, has retained only the genera *Dipylidium* Leuckart (1863), *Diplopylidium* Beddard (1913), and *Joyeuxia* Lopez-Neyra (1927), later renamed *Joyeuxiella* Fuhrmann (1935).

Many tapeworms have been described and placed in the genus *Dipylidium*. Numerous species, formerly in this genus, have been transferred to the related genera *Diplopylidium* and *Joyeuxiella*. Witenberg attempted to clarify the synonymy of the *Dipylidiinae*. He concluded that *D. caninum* was the only valid species of the genus *Dipylidium*, listing forty-one synonyms; the validity of *D. buencaminoi* was regarded as uncertain. His contribution is valuable and more attention to this subject is required.

A description of the internal anatomy of *D. caninum* and a review of observations on its life history were included by Diamare (1893) in his monographic treatise on the genus *Dipylidium*. Previously, Steudener (1877) had made some observations on the microscopic structure of the body-wall, and of the sexual organs and their ducts. Moniez (1881) described spermatogenesis, segmentation of the ovum, and formation of the embryonic coverings. After fertilization of the ovum, its peripheral layer of cytoplasm becomes modified into a vitelline membrane. Segmentation produces a mass of similar cells, the outer layer of which delaminates, undergoes granular degeneration, and forms a thick envelope between the embryo and the vitelline membrane. The cells of the embryo are delimited from the granular

envelope by a thin layer which, Moniez suggested, is perhaps secreted by the embryo. A muscular mass, into which the bases of the embryonic hooks are inserted, was described. Several stages of segmentation, believed to be abnormal, were noted.

The pathological effects of *D. caninum* in dogs and cats have been greatly underestimated by many authors. Schiefferdecker (1875) noted an instance in which many individuals of *Dipylidium* had tunneled beneath the intestinal mucosa of a dog until their scolices and adjoining immature segments were completely covered. Railliet (1892), and later Henry & Lebois (1923), observed segments of *Dipylidium* in diseased anal glands of dogs. A specimen 12 centimeters long was found in the gall-bladder of a dog that died from an intestinal and liver ailment (Vogelsang, 1922). The presence of a proglottid containing many egg-capsules, encysted in the wall of the large intestine of a cat, was reported by Brumpt (1926). The cat had been experimentally infected with amoebae. Since no amoebae were present in the cyst, it was considered likely that the proglottid was established in the intestinal wall before the experiment. A hemorrhagic enteritis was observed by Venard & Ellis (1933) in those dogs whose intestines harbored one hundred or more worms. This condition appears to be due to habitual burrowing into the mucosa by the cestodes and perhaps also to invasion of the lesions by bacteria.

The presence of *Dipylidium* in man is often dismissed with the statement that no ill effects usually result. Brandt (1888), however, described the pathological effects of two typical cases which he treated. Symptoms included loss of weight, weakness, loss of appetite, vomiting, abdominal pains, constipation, biliousness, labored breathing, and nervousness. When the proglottids left the anus they caused severe itching and pains. These symptoms increased to a maximum, and then a spontaneous loss of a large number of proglottids and partial strobilas was followed by relief. A month later the symptoms reappeared and the cycle was repeated. After treatment with anthelmintics and recovery of thirty complete worms from one patient and forty-eight from the other, the symptoms disappeared. It is sometimes implied that only children become infected, but Zschokke (1903) has pointed out that adults, as well as children, may harbor large numbers of these worms. The number of parasites in an infection, accompanied by the production of large numbers of proglottids, indicate that man is a favorable host. The nature of its effect on man shows, at least in some cases, that it is a parasite of medical importance.

Life-history of Dipylidium caninum

Ordinarily proglottids do not disintegrate in the intestine, but emerge intact. The segments that contain ripe, infective eggs either pass out in the feces or migrate actively out of the anus of the host. Due to the high incidence and wide geographic distribution of this tapeworm, many investigators believed that it had a direct life-history.

The first evidence of an intermediate host in the life-cycle was noted by Melnikow (1869) while working in Leuckart's laboratory. He found a cysticercoid in the body-cavity of the biting louse *Trichodectes canis* Degeer; the scolex, when exposed by pressure on the cyst, greatly resembled the scolex of *D. caninum.* In order to confirm his discovery, Melnikow fed *Dipylidium* eggs to *T. canis* and a week later he recovered four onchospheres from one insect and one "flask-shaped" individual from another specimen. These were evidence that the louse served as an intermediate host. Previously, he had vainly attempted to infect cockroaches by feeding them *Dipylidium* eggs; and similar experiments on cockroaches, flies, and maggots made by other investigators had always given negative results.

The intermediate host discovered by Melnikow did not have a wide enough geographic distribution and incidence of infection to account for the frequent occurrence of the cestode in dogs. In addition to the louse, another host with a distribution and incidence correlated with that of the tapeworm was indicated. The dog flea fulfilled the necessary requirements and after a long search, Grassi (1888a) found the cysticercoid stage in the abdominal cavity of an adult dog flea. Later in the same year (1888b) he reported further studies which formed the basis of extensive reports by Grassi & Rovelli (1889a, 1889b, 1892). These investigators described the stages which occur in the adult flea. Furthermore, Grassi (1888b) reported that he and Rovelli had found the cysticercoid in the human flea, *Pulex irritans* Linnaeus. Galli-Valerio (1911) found a cysticercoid, which he regarded as the larva of *D. caninum,* in the human flea. The discovery by Grassi that the dog flea could serve as the intermediate host was confirmed by Sonsino (1889) who, on two occasions, found the cysticercoid while dissecting several hundred fleas in connection with a study of filariasis.

The method by which the flea, a blood-sucking parasite, acquires the infection remained to be solved. The adult flea could not ingest *Dipylidium* eggs because the mouth-parts would not admit objects of

such size. Sonsino suggested two possibilities. The first was that the egg hatched and liberated an onchosphere which entered the abdominal cavity of the adult flea by actively penetrating the soft portion of the abdominal wall between the sclerites. The second possibility was that flea larvae became infected by ingesting eggs. Flea larvae have mouth-parts of the chewing type and an oral opening large enough to permit passage of eggs. The eggs would hatch in the intestine of the flea larva, and the onchospheres, by means of their hooks, would penetrate the intestinal wall thus gaining entrance to the body-cavity. The first hypothesis was not likely; the latter was plausible. It remained for Joyeux (1916) to demonstrate that *Ctenocephalides canis* (Curtis) and *Pulex irritans* become infected during their larval instars. Another intermediate host, *Ctenocephalides felis* (Bouché) was added by Chen (1934).

Comparative Anatomy of Onchospheres

The onchosphere of *Dipylidium caninum* has been only superficially described (Melnikow 1869). The anatomy of the onchospheres of some other cestodes has recently been studied critically. It is necessary, for comparative purposes, to review these studies briefly.

Vogel (1929, 1930) showed, by means of the methyl-green-pyronin staining technique, that the onchosphere of *Diphyllobothrium latum* consists of two types of cells, termed "plastin" and somatic cells. An onchosphere contains four to twelve plastin cells when it emerges from the embryonic coverings. In a four-day larva the number has increased to twenty or thirty and in a seven-day larva the interior of the body is entirely filled with this type of cell. Each nucleus contains a large nucleolus. The nucleolus and cytoplasm stain red and the rest of the nucleus is colored light green. The plastin cells, with the faculty of rapid division, were considered germinal in nature, and similar ones were demonstrated in the miracidium of *Fasciola hepatica.* The somatic cells are numerous, but do not divide rapidly and hence contribute little bulk to the developing larva; their fate is not definitely known, but they may form parenchyma and muscle-cells. The nuclei of somatic cells stain green while the cytoplasm remains colorless. In addition to these two types of cells, the onchosphere contains two flame-cells, and muscle-fibers which operate the hooks. In the vicinity of each flame-cell are many small granules.

The embryo of *Archigetes* consists of germinative and somatic cells (Wisniewski, 1930). The germinative cells are larger and divide less

rapidly than the somatic. There is no definite cell-arrangement in young embryos, but in older ones the somatic cells lie at the periphery and the germinative cells are located in the center of the body. The further history of the two types of cells is shown in the following table from Wisniewski (1930, page 88).

TABLE I

<table>
<tr><th>Age of Larva</th><th colspan="4">Type of Cells</th></tr>
<tr><td>Early embryo
0 064–0.94 mm</td><td colspan="2">Germinative cells</td><td colspan="2">Somatic cells</td></tr>
<tr><td>Later embryo
0.28–0.36 mm.</td><td>Germinative cells</td><td>Germinative-somatic cells</td><td colspan="2">Somatic cells</td></tr>
<tr><td>Further development</td><td>Sex-organs</td><td></td><td>Parenchyma</td><td>Muscles
Nerves
Excretory system
Sexual ducts</td></tr>
</table>

Michajlow (1933) described seven different types of cells in the onchosphere of *Triaenophorus nodulosus;* they are distinguished by their morphology and staining reactions in Mallory's, methyl-green-pyronin, and iron-haematoxylin techniques. The oncosphere consists principally of somatic cells, whose nuclei are green and cytoplasm colorless in methyl-green-pyronin preparations. Near the somatic cells, but less numerous, Michajlow distinguished lambda cells, much resembling the former but distinguishable with Mallory's stain. The nuclei of the somatic cells stained red to yellow, whereas the nuclei of the lambda cells stained blue. Also, in iron-haematoxylin preparations the plasma of somatic cells remained colorless, while that of lambda cells was stained light red. Distributed throughout the body of the onchosphere, but more concentrated in the cortical area, were nine to twenty-three cells whose nuclei were stained bright red-brown, nucleoli red, and cytoplasm red by the methyl-green-pyronin technique. These were accepted as the equivalent of the plastin cells described by Vogel and the germinative cells described by Wisniewski. Near the germinative cells in a subcuticular position Michajlow recognized others which he called germinative-somatic cells, characterized by several nucleoli in each nucleus. Their plasma remained colorless in methyl-green-pyronin and iron-haematoxylin preparations, whereas the plasma of the germinative cells was colored red by the first stain and deep pink or red by the second. Granular cells of two different sizes were located in the posterior half of the onchosphere. Flame-cells, and muscle-cells attached to the hooks, were described.

The larvae of *Cittotaenia*, as described by Stunkard (1934), are about one third to one half the size of those of *Archigetes*, *Diphyllobothrium*, or *Triaenophorus* and hence less favorable for study. In both living and fixed specimens, by use of the methyl-green-pyronin technique, two types of cells could be distinguished. The onchosphere is composed of numerous, small somatic cells and ten to twenty larger cells which correspond to the plastin cells described by Vogel. Refractive granules localized into two areas, as in *Diphyllobothrium*, were noted. Flame-cells were not observed.

Cysticercoid of Dipylidium caninum

The cysticercoid was discovered and described by Melnikow (1869). The one observed by him was nearly spheric in shape, gray in color and contained numerous calcareous corpuscles. It was described as enclosed in a thick, colorless, transparent cyst. Under the microscope the suckers and scolex were distinguished as muscular structures, but the remainder of the body, except for an occasional muscle-cell, was described as a mass of homogeneous tissue. A large excretory pore was noted in the wall opposite the inverted scolex. Melnikow pointed out that this was different from the usual tapeworm cysticercus in that it did not possess a caudal vesicle; however, he did not propose a new name for it. The description of the cysts from fleas, by Sonsino (1889) is similar to that of Melnikow.

Grassi & Rovelli (1892) studied the development of the cysticercoid in the adult dog flea, and compared (1889a, 1889b) it to the cercaria of the Trematoda. Their observations began with the stage in which a conspicuous cavity was present. The cavity, called "lacuna primitiva" by these authors, was formed either by the destruction of cells or by their migration. At this time the organism consisted of cells which were similar in size and shape, but in later development two kinds were evident. One type consisted of a few large cells and the other of numerous small ones. Observations on the formation of calcareous corpuscles, nervous, muscular, and excretory systems, and scolex were recorded.

The cysticercoid was named *Cryptocystis trichodectes* Villot (1882). It was later transferred by Stiles to the genus *Cercocystis* Villot (1882). It was also described as *Cryptocystis pulicides* Campbell & Lacroix (1907). Since the adult form was described and named before the early stages, names proposed for the latter disappear as synonyms.

MATERIAL AND METHODS

The dog flea was employed as the intermediate host. A stock of adult fleas was maintained on a long-haired, small dog which was free from cestodes during the course of experiments. The flea eggs which did not adhere to the dog, dropped on a pan which formed the bottom of the cage. They were collected in large numbers from the pan with a small moistened camel's hair brush. Eggs thus collected were placed in Petri dishes filled to a depth of three millimeters with fine, washed, autoclaved sand. The Petri dishes were stored on a shelf in a tightly fitting wooden box 8 by 10 by 16 inches in size. A dish seven inches in diameter filled with water was kept in the box for humidity; occasionally a drop of water was added directly to the sand in the Petri dishes. The box was kept at room temperature. The larvae were fed fragments of dog biscuits and dried beef-blood or dog-blood. Handled in this way approximately 75 per cent of the eggs produced adult fleas. The life-cycle from egg to adult required twenty-five to thirty days.

Previous to feeding cestode eggs, flea larvae were isolated into lots of desired numbers and food was withheld for twenty-four hours. Gravid proglottids, obtained from dogs freshly killed by etherization, were covered with Ringer's solution and teased apart in watch crystals, and the eggs were then concentrated in a few drops of the liquid. Dried and powdered blood was added to the concentrated eggs to form a soft mass which was quickly ingested by the larvae. This method produced a much higher percentage of infection than any other method tried.

All dogs and cats used as hosts in the experiments were free from cestode infection, as determined by daily examinations over a period of three weeks. In addition each animal was treated with arecoline hydrobromide ten days before an experiment, and again examined for cestodes.

Adult cestodes, early stages, and eggs have been studied alive and after fixation. The fixatives most commonly employed were Bouin's, Flemming's, and Zenker's. A mixture of 7 parts saturated aqueous solution of corrosive sublimate and 3 parts of 95 per cent ethyl alcohol was found to be an excellent fixative for larval cestodes dissected out of adult and pupal fleas. The stains employed for sections and larvae were Heidenhain's iron-haematoxylin, usually counterstained with erythrosin, Flemming's triple stain, Mallory's triple connective-tissue stain, and the methyl-green-pyronin technique described by Vogel (1929). It was found necessary to use the Pappenheim pyronin

and methyl green prepared by G. Grübler. These two stains, used separately and mixed in various proportions and concentrations, in my studies have been the most useful ones as vital dyes. Alum carmine and Ehrlich's acid haematoxylin were used for whole mounts of adult cestodes.

INFECTION OF FLEA LARVAE

Flea larvae become infected by the ingestion of tapeworm eggs which escape from the host in the proglottid. Gravid proglottids become detached, usually one at a time, from the tapeworm strobila, and escape from the host either actively by creeping out of the anus or, less frequently, passively in the feces. Proglottids which creep out of the anus usually adhere, upon desiccation, to hairs near the anal region. Those which are carried out in the feces crawl about over surrounding surfaces. On rare occasions eggs are released inside the host; however, this phenomenon is usually associated with constipation. As noted, the fresh proglottid has the power of locomotion when it leaves the host. It may move several inches in an hour if it is placed on damp filter-paper, but cannot travel so far on a dry surface. Shedding of the eggs is conditioned by the two factors of movement and of desiccation. When a proglottid begins to dry, which requires but a few minutes in the arid atmosphere of a steam-heated room, a rupture appears in the body-wall near the end which was distal to the scolex. This end trails during locomotion, and the movements of the segment expel the eggs through the opening.

It is difficult to infect flea larvae with eggs contained inside the proglottid. Its substance is viscous and flea larvae adhere when they attack the material. Many larvae, after attempting to feed, are unable to free themselves and die attached to the proglottid. The incidence of infection is low in those larvae that survive. It is likely, in nature, that larvae are infected only by ingesting eggs that have been shed by the proglottid.

The onchospheres, in eggs released from the proglottid, soon lose their ability to infect flea larvae. Eggs allowed to dry for twenty-four hours retain their shape but very few are infective. At the end of forty-eight hours no infection was produced when many eggs were fed to larvae. These data show that under natural conditions the eggs, in order to be infective, must be ingested shortly after they are liberated from the proglottid.

MORPHOLOGY AND DEVELOPMENT OF THE EGG

The *Dipylidium* egg in a gravid proglottid consists of an infective onchosphere, 25 to 30 microns in diameter, with its coverings. The fresh egg (FIGURE 13) is spheric in shape with a diameter between 35 and 60 microns. Fixation may destroy the spheric shape (FIGURE 12) and also cause slight shrinkage. The ripe eggs are bound together into bundles of two to sixty-three, with the majority of bundles containing fifteen to twenty-five eggs. These collections of eggs are called egg-capsules (FIGURE 18). Sometimes eggs occur singly and such eggs are enclosed in an envelope of capsule material.

The covering of the onchosphere consists of two distinct envelopes. The inner envelope, which is closely applied to the onchosphere, is the embryophore (FIGURE 13, *em*); the outer is the yolk-shell (FIGURE 13, *ys*). Between the two lies a layer of albuminous material (FIGURE 13, *am*). In order to explain the nature of these coverings it will be necessary to describe their formation.

The mature unfertilized ovum (FIGURE 1) is 15 microns in greatest diameter. It contains a spheric nucleus with a diameter of 7 to 9 microns. The shape of the cell is usually ovoid, but it may be irregular due to contiguity with other ova in an ovarian follicle. The spermatozoon appears to be simple in structure and each end tapers to a point. When alive, its length is approximately 150 microns and the diameter is slightly more than one micron. Apparently the entire spermatozoon enters the ovum. After fertilization (FIGURE 2) the ovum receives yolk from the vitelline gland. The yolk-cells (FIGURE 7) measure approximately 6.5 microns and contain eccentrically located nuclei 3 to 3.2 microns in diameter. Each ovum receives one yolk-cell and the two cells pass into the shell-gland. The yolk-cell, with the exception of the nucleus, disintegrates immediately. The shell-gland secretes a thin covering, the true shell (FIGURE 3), about the egg. The shell is deciduous, and so is absent from the mature egg; it must not be confused with the coverings of the onchosphere which are formed later The fertilized ovum, enclosed with its supply of yolk in the shell, passes into the uterus.

Segmentation begins as soon as the egg reaches the uterus. The first cleavage results in the formation of two approximately equal blastomeres (FIGURE 4), and simultaneously the shell enlarges, becomes thinner, and forms a loose vesicle around the blastomeres. At this time a third object becomes visible, the nucleus of the yolk-cell, and it

will contribute to formation of the yolk-shell. Near the yolk-cell nucleus (FIGURE 4) are several small bodies, apparently yolk particles, which vary in size, shape, and number. As interpreted by Moniez (1881) the yolk-cell nucleus is a blastomere resulting from abnormal segmentation, and two of the smaller bodies were thought to be polar bodies. Of the two blastomere nuclei the larger is 8.5 to 9.6, the smaller 7.5 to 8.5 microns in diameter. The size of the two-celled stage is approximately 18 by 24 microns.

The blastomere containing the larger nucleus does not divide; its nucleus increases slightly in size and becomes vesicular in appearance. The cytoplasm contains many yolk-granules. The entire cell disintegrates and contributes to the formation of the yolk-shell.

The other blastomere undergoes segmentation to form three macromeres and a number of micromeres; the former contribute to the formation of the yolk-shell, the latter form the embryo and the embryophore.

The yolk-shell is formed from four macromeres, the yolk-cell nucleus, and portions of the yolk (FIGURE 6). In mature eggs it is 2.5 to 3.2 microns thick and forms the outermost covering of the embryo. Hence in the literature this structure is usually called the shell.

After the shell has begun to form, five peripheral micromeres are segregated from the mass of micromeres, become flattened, and unite to form an envelope (FIGURE 8) around the other micromeres. This envelope is the embryophore, which encloses the cells that develop into the onchosphere. The nuclei of the cells which form the embryophore disintegrate. In mature eggs (FIGURE 13, *em*) this layer, which is closely applied to the onchosphere, seldom measures more than 1.5 microns in thickness, except in some regions where fragments of nuclei are located.

Irregularities in formation of both yolk-shell and embryophore are common. Occasionally more than four macromeres are present during formation of the yolk-shell. This condition appears to be due to division of the first-cleavage blastomere, which ordinarily does not divide. It is unlikely that extra macromeres are incorporated into the yolk-shell, since isolated macromeres are sometimes seen between the embryophore and yolk-shell surrounding fully developed onchospheres. In rare instances, the embryophore appears to arise by delamination and to be composed of more than five cells. Whether these cases result in abnormal coverings or eggs, is not known. It is probable, however, that these coverings are not formed with the exactness described for species of *Taenia*.

The albuminous layer (FIGURE 12, *am*) between the yolk-shell and the embryophore consists principally of a uterine fluid which diffused through the yolk-shell during its formation. This fluid contains many yolk-granules, lipoid globules, and portions of the macromeres that formed the yolk-shell; macromeres, not incorporated into the yolk-shell, are sometimes present. In fresh eggs the suspended particles move about from place to place.

The eggs are held together by a secretion from the uterus. As soon as the yolk-shell is formed, the capsular material begins to collect about the eggs, binding them into bundles. This substance is at first nearly transparent, but it becomes translucent and gradually acquires a pink tint as the proglottid ripens. Gravid proglottids, accordingly, show a deep pink or light red color which is destroyed by fixation or preservation. The capsular material is adhesive when fresh, but upon desiccation it becomes tough and then brittle. It colors light blue with Mallory's stain and shows no peculiar structural characteristics. The egg-capsule has a smooth outer surface and usually an elliptic outline (FIGURE 18). The number of eggs in a capsule determines its size, which may reach 130 by 280 microns.

The *Dipylidium* egg has been studied in serial sections. In the onchosphere two types of cells are readily recognized by differences in morphology and staining reactions. The cytoplasm of one type stains poorly with the usual cytoplasmic dyes, but that of the other type stains deeply with pyronin. Nuclear differences are striking (FIGURE 14), and it is mainly upon these differences that the cells are recognized and classified. The number of cells in the mature onchosphere varies from seventy-five to one hundred, and the size of the larva varies directly with the number of cells. Each egg contains about forty cells (FIGURE 9), 3 to 5 microns in diameter, with spheric or elliptic nuclei that stain deeply with Heidenhain's iron-haematoxylin, green in methyl-green-pyronin, and red with Mallory's stain. These nuclei measure from 2 to 3 microns in greatest diameter. The smaller nuclei are always stained more intensely than the larger ones. There is no definite nucleolus, but small irregularly shaped deeply-staining granules may be present. At first sight the larger and smaller nuclei appear quite distinct, but careful study reveals a complete series of sizes corresponding with the differences in staining reactions. I have assumed the larger nuclei to have the same origin as the smaller ones and to represent a later stage of development, since the former are not present during early segmentation or in newly formed onchospheres, and the latter gradually disappear as the onchospheres increase in age.

Around the smaller nuclei, Mallory's stain reveals a cytoplasm which often appears light blue, whereas the cytoplasm surrounding larger nuclei remains colorless. This type of cell corresponds to the somatic cells described by previous investigators in young cestode larvae. They are evenly distributed throughout the *Dipylidium* onchosphere.

In addition to the somatic cells, there is an approximately equal number of larger cells, up to 10 microns in diameter, with nuclei measuring 3 to 4.8 microns in diameter. Each nucleus contains one large nucleolus, several smaller nucleoli, or numerous small spheric granules, all of which, like the cytoplasm, are stained deep red with pyronin. Furthermore, just within the nuclear membrane are numerous fine, deeply-staining granules. The rest of the nuclear material remains colorless. These cells may be divided into two types.

The cells of one type (FIGURE 10) contain spheric to ovoid nuclei, each with a very conspicuous nucleolus. The nucleolus is stained deep red with pyronin and intense black with Heidenhain's iron-haematoxylin; it is approximately one micron in diameter. The nuclear material surrounding the nucleolus is stained pale green in methyl-green-pyronin and light gray in iron-haematoxylin preparations. The nuclear membrane is distinct and many fine granules lie near its inner surface. The granules and membrane stain deeply and the same color as the nucleolus. The layer of cytoplasm surrounding the nucleolus is usually thin, but rarely it is fairly thick, and is stained red with pyronin and blue with Mallory's stain. Approximately thirty of these cells are distributed more or less uniformly throughout the onchosphere. Four or five cells occupying a central position in each larva are larger and more conspicuous than the others; these are identified with the plastin cells of Vogel and the germinative cells of Wisniewski.

Of the other type (FIGURE 11) there are ten to fifteen cells. The cytoplasm remains practically colorless, except when treated with pyronin. The nuclei, which have two or more nucleoli, or numerous fine granules, are usually circular in outline. The nucleoli and granules are always stained deep red with pyronin and Mallory's stain, and intense black with Heidenhain's iron-haematoxylin. Halos of lightly stained nuclear material may often be noticed around nucleoli when two to four are present in a nucleus; the remaining nuclear material is stained light blue with Mallory's stain. The nuclear membrane appears dark red with pyronin and Mallory's stain, and black with Heidenhain's iron-haematoxylin. The larva usually contains two or three cells with two nucleoli, three or four cells with three nucleoli, and

four or five cells with numerous granules; these cells, especially those with numerous granules, are located in the central region of the larva. I have not been able to classify these cells into different types; they blend through a graded series with the germinative cells. The single large nucleolus of the germinative cell apparently breaks up into smaller units, thus giving rise to cells with two or more nucleoli or numerous granules; these do not appear until the larva is quite mature. I shall call the cells with more than one nucleolus "germinative-somatic cells," in agreement with the name applied by Wisniewski to the cells which originate from the germinative cells in *Archigetes*.

The infective larva contains, in addition to the cells described above, the embryonic hooks, yolk-fragments, and an intercellular fluid. The six embryonic hooks frequently appear to lack any definite orientation (FIGURE 13). The few yolk-globules appear as deeply stained bodies with diameters of one micron or less. In the intercellular spaces there is a small amount of fluid which is stained deeply with pyronin and contains numerous very fine granules.

HATCHING OF THE ONCHOSPHERE

The onchosphere normally does not escape from the egg-coverings until the egg is ingested by a flea larva. It hatches in the fore- or mid-intestine and begins immediately and actively to penetrate the intestinal epithelium of the larva. The method of hatching is here described (1) as induced under the microscope by artificial means, and (2) as it occurs normally in the host.

If fresh egg-capsules are teased from a gravid proglottid and placed in distilled water, many eggs at the periphery of the capsule will have cracked yolk-shells thirty minutes later. Escape from the aperture in the yolk-shell is dependent upon active movements by the onchosphere, which does not escape until the embryophore also is ruptured. From fifteen to thirty minutes after the yolk-shell ruptures, the embryophore follows suit and the onchosphere then leaves the coverings and moves slowly over the substratum. A high percentage of eggs will also hatch in tap-water. Eggs in the interior of a capsule do not hatch, since the egg-capsule protects them. If capsules are placed in isotonic salt solutions the yolk-shells do not break and hatching does not occur.

The hatching of eggs under a coverglass cannot be studied satisfactorily unless the glass is supported to relieve pressure on the capsules. The pressure of a coverglass will almost always cause hatching, due to rupture of the embryophore and the yolk-shell in the same plane. This type of hatching (FIGURE 17) may be attributed errone-

ously to hook-movement, since the onchosphere is often oriented so that the hookbearing portion is the first to escape.

Hatching, as described above, is not dependent upon movements of the onchosphere's hooks. The hooks in eggs placed in distilled water or tap-water seldom show movement, but nevertheless many eggs hatch unless they are located in the interior of the capsule. Eggs in isotonic salt solutions never hatch, although hooks may be in almost continuous motion for as much as four hours with no observable effect. The rupture of the yolk-shell and embryophore appears to be due to pressure caused by imbibition of water from a hypotonic medium.

The process of hatching, as it occurs in the intermediate host, has been studied by dissecting intestines out of flea larvae at short intervals after feeding and observing the eggs in the intestinal contents. Flea larvae become infected by ingesting eggs obtained by chewing on egg-capsules. The mouth-parts of the insects usually rupture the yolk-shells; the flea's digestive juices dissolve the shell and vigorous churning movements of the gut aid in breaking it into pieces. The onchosphere leaves the yolk-shell enclosed in the embryophore (FIGURE 16) and moves about, which is contrary to observations on those artificially hatched, and the hooks are continually moved. The embryophore, which has hitherto been closely applied to the surface of the onchosphere, begins to stretch and enlarge, due to the digestive action of the intestinal juices, and a space appears between the onchosphere and the embryophore. Rupture of the embryophore follows its dissolution by the intestinal fluid of the flea, although the activity of the onchosphere may assist in liberation from the covering.

Hatching involves a series of steps which occur in a definite sequence, and may be reviewed here. The first indication is a rupture in the yolk-shell. Onchosphere movements and hook activity are not responsible for this initial phase, since the hooks are never in contact with the external covering. It has been noted that most yolk-shells are ruptured by the flea larva during feeding, but this process is not a necessary prelude to hatching, because the digestive juices of the flea are capable of disintegrating the yolk-shell. The onchosphere leaves the yolk-shell enclosed in the embryophore (FIGURE 16), from which it escapes within a short time. On several occasions, a yolk-shell containing an empty embryophore has been found, showing that hatching similar to that artificially induced (FIGURE 17) may also take place. Onchospheres may be injured by the mouth-parts of the flea, as is shown by the occasional occurrence of isolated hooks in the intestine. Practically all eggs are hatched within thirty minutes after ingestion, although a few remain intact for an hour and their fate is not known.

MORPHOLOGY OF THE EMERGED ONCHOSPHERE

Studies have been made upon newly emerged onchospheres, both from eggs hatched artificially and from eggs hatched in the intestine of the flea larva. Living specimens have been studied for hours both unstained and with the aid of vital dyes. The young onchosphere is very active. The hooks are continually extended and retracted and the entire outline of the body assumes different shapes in rapid succession. The rate of forward movement is slow. The hook-bearing end is always foremost in progression and for that reason is considered the anterior end. At rest the onchosphere is spheric or slightly flattened in front. Movement is initiated by the extension of the median pair of hooks, and the anterior end becomes pointed. The hooks are elevated as they are extended, and after complete extension they execute a downward cutting movement; at this time the lateral pairs are extended synchronously with the tips pointed anteriorly, and execute a horizontal rowing movement with the cutting edges directed posteriorly. The body now elongates, often with a median constriction. When the hooks make contact with the substratum, the posterior part of the body is pulled forward until the larva becomes roughly triangular in outline. With retraction of the hooks the body again becomes spheric and the cycle (FIGURES 20 to 24) is repeated.

The onchosphere (FIGURE 25) is bilaterally symmetric with the longitudinal axis passing between the median pair of hooks. It is also differentiated on a dorso-ventral axis, as demonstrated by its progress in locomotion with the blades of the hooks directed forward and downward. The hooks are arranged in three pairs. The median pair is located on the anterior tip of the onchosphere and the two other pairs are situated antero-laterally and slightly obliquely to the median pair. Members of the median pair are parallel when at rest in the retracted position. Members of the lateral pairs are close together at the ends which are embedded on the onchosphere. The hooks are always extended and retracted in pairs, but any pair may move independently of the other two pairs. The members of a pair may move independently of each other while in the extended position. In order to account for the independent movements of the hooks, without any noticeable change in bodily shape of the onchosphere as a whole, it must be assumed that contractile fibers are present to operate them, but such fibers have not been seen in live material, unstained or vitally stained, or in specimens stained with dilute aqueous solutions of picric acid.

Each hook (FIGURE 19) consists of three portions: a handle, a blade and guard. The handle is that portion deeply embedded in the onchosphere. It is straight, and elliptic in cross-section, with a length of 6.5 microns. The blade is 4 microns in length, and consists of the curved portion which protrudes from the onchosphere when the hook is extended. At the junction of the blade and handle is the guard, at right angles to the handle and on the same side as the cutting edge. The guard marks the limit to which the hook may be protruded, and the hook may swing on it as a pivot. The entire hook measures 10.5 microns in length.

Only one variation from the normal number of hooks was noted in the thousands of onchospheres observed during a period of four years. This specimen, which measured 35 microns, possessed twelve hooks of normal size. Two pairs were located at each place where normally only one pair is present. This individual moved about and was observed at intervals for more than an hour. It had been ingested by a flea larva and was recovered from its intestine.

The onchosphere does not increase in size immediately after leaving the egg-coverings. It tends to retain its spheric shape, which interferes with observation of the cellular elements, but on occasion it may change its form greatly and, when flattened, observation is facilitated. It is enclosed within a very clear, shiny covering of cuticula about one micron in thickness. The onchosphere is light greenish blue and cells near the surface appear as lighter areas. Small granules are scattered among the cells throughout its interior.

The study of living unstained onchospheres gives little clue to their cellular constitution. The nuclei of germinative cells near the surface appear as light, transparent areas in the median or posterior portions of the body. Usually two or three nuclei are distinct. Often two nuclei lie in posterolateral positions so that a definite bilateral organization is apparent (FIGURE 25). If the onchosphere is compressed slightly under the coverglass the cells become more distinct (FIGURE 26). Five or six germinative cells and ten or twelve somatic cells may be seen. Only cells on the upper surface are distinguishable.

With the use of methyl-green-pyronin as a vital stain the cellular organization of the onchosphere can be studied readily, and stained specimens may be kept under observation for several hours. Five to ten germinative cells are evident within a few minutes after the stain is applied. Some minutes later the interior of the body becomes a deep red, due to coloration of the cytoplasm of germinative and germinative-

somatic cells. The intercellular material, which also stains red, has increased in amount. The somatic cells, mainly subcuticular in position, are obscured by the pyronin but are stained well in specimens treated with dilute methyl green.

Flame-cells have been described in the onchospheres of two species of *Diphyllobothrium* and in *Triaenophorus nodulosus*, but attempts to demonstrate them in *Dipylidium* have been unsuccessful. Numerous larvae have been studied in tap-water, in distilled water, and in albumen-water, and in salt solutions of varying concentrations at different temperatures and degrees of compression, with direct and indirect illumination under high magnifications.

The fragile onchosphere will live for a few minutes in tap-water or distilled water, but movement soon ceases and disintegration occurs within an hour; they will live in Ringer's solution for several hours, but sodium chloride, alone, in dilute concentrations (0.7%, 0.5%, 0.25%) is highly toxic. Numerous specimens in Ringer's solution have been studied for three hours in sealed preparations under the oil-immersion lens.

THE ONCHOSPHERE AND CYSTICERCOID IN THE FLEA

The growth of the onchosphere and its metamorphosis into the cysticercoid are influenced by the development of the host. Important factors which affect the host are food, temperature, and humidity, and they modify the rate of development of its parasites. All flea larvae were reared on an identical diet, but the temperature and the humidity varied considerably. It may be stated that generally the onchospheres grow but little in the flea larva, considerably during the pupal period, and transform into the cysticercoid after the adult begins to feed on a suitable host.

The Onchosphere in the Flea Larva

The onchosphere, which is liberated in the fore- or mid-intestine of its host, moves about in the characteristic fashion described above until the hooks become engaged in the epithelial cells of the flea's gut. Penetration of the intestinal wall appears to be mechanical and due entirely to activity of the hooks. Although Chen (1934) has pointed out the possibility that histolytic juices might be secreted by the onchosphere, there is no evidence to support the suggestion. The actual duration of penetration has not been timed accurately, due to difficulties in technique. Onchospheres have been dissected from the body-

cavity two hours after feeding, and none has ever been found in the intestinal tract twenty-four hours after feeding.

After reaching the body-cavity the onchospheres continue their activity and migrate to all regions among the host organs. They seem to wander continually unless, as sometimes happens especially in heavy infections, they penetrate the tissues and fail to develop. They gradually collect in the posterior end of the host and, after the fifth day, are seldom found elsewhere. Their collection in this region appears to be passive on the part of the parasites; the movements of the internal organs of the host are greater in the anterior than in the posterior region, and the parasites tend to remain in the region of greatest quiescence.

Onchospheres dissected from the body-cavity within twenty-four hours after infection differ in appearance from those newly hatched. The hooks lie nearer the surface, and being more evident, present the illusion of an increase in size. The symmetry of the body is more distinct. An indentation is usually present on each side between the median and each lateral pair of hooks. The length of the body is slightly greater than the width. The onchospheres are most active at this stage of development and always move with the hook end foremost.

The somatic cells gradually disappear and after the fourth day many individuals show none when treated with methyl green. Serial sections show but four or five of these cells located near the hooks. Older onchospheres lack this type of cell. The germinative-somatic cells are sometimes absent after the third day and in other specimens only an occasional one (or two) is present. However, this type of cell may be found at a later period and, due to their fluctuating numbers and presence during periods of rapid germinative cell multiplication, it is suggested that they are germinative cells in which the single large nucleolus becomes fragmented. The cells in the interior of the onchosphere come into view as the somatic cells disappear. At first only a few are visible, and in living four-day onchospheres seven to ten germinative cells, arranged in groups of two or three, can be distinguished. Serial sections, however, show about forty of these cells. While there has been only a slight increase in their total number, the individual cells are larger, and spheric ones may measure 10 microns in diameter. Seven to ten of these cells have nuclei 4.8 to 5.0 microns in diameter and contain nucleoli as large as 1.9 microns. These cells are distorted by fixatives and the cytoplasm is poorly stained, even with pyronin. Considerable intercellular fluid is present. It contains numerous minute irregular granules and many refractive lipoid globules. Simi-

lar globules adhere to the cuticula; they are probably derived from the insect larva, since many fat-cells of the host are ruptured as the flea is dissected and some of their contents adhere to the outside of the onchosphere.

The onchospheres gradually increase in size due to the rapid division of the germinative cells. The anterior indentations, lateral to the median pair of hooks, disappear. The germinative cells are disposed in two groups, of eight or ten cells each, which are conspicuous in the living condition (FIGURES 29 and 30). These groups lie nearer the ventral than the dorsal surface, hence at this time the larva shows a distinct dorso-ventral differentiation. Surrounding the two large groups are other cells, in groups of two or three. The intercellular fluid has increased in amount and the small granules in it are exceedingly numerous, especially in the area between the two large groups of cells. Occasionally this stage is not a conspicuous one. If old flea larvae are infected, the onchospheres will be only two to five days of age when the prepupal period is reached. Such onchospheres become spheric, as mentioned below, and the condition described above is obscured.

At ten days of age the onchospheres average approximately 65 microns in diameter, the size varying with the intensity of infection, the location of the parasite, the temperature, and, undoubtedly, the response of the host's defensive mechanism. If the host harbors forty to fifty parasites, which may be considered the maximum, the smallest ones frequently are one half the size of the largest. The onchospheres grow more rapidly in lighter infections with several to ten parasites. Those which penetrate the organs of the host are not as large as those in the body-cavity, and it may be that they do not develop into cysticercoids in such locations. Increase in temperature accelerates growth of the onchospheres.

Approximately eleven days after moderate infection of young flea larvae they are in the prepupal stage. The onchospheres become spheric (FIGURE 28) and the hooks lose their orientation until they are no longer recognizable as three pairs. The cells move from place to place and the intercellular fluid flows about as the onchosphere exhibits feeble amoeboid movements.

The Onchosphere in the Flea Pupa

The spheric larva is light gray when the host enters the pupal period, and ranges from 40 to 80 microns in diameter. During the pupal period of the host, growth of the cestode is rapid, due to a large

increase in the total number of cells and to the production and accumulation of a large amount of fluid. The hooks, limited to one hemisphere, are located at the surface and the blades may protrude. One or more of them may be lost during this stage.

From two to several days after pupation of the host, depending upon the extent of the infection, a small cavity, the "lacuna primitiva" of Grassi & Rovelli (1892), appears in the center of the onchosphere. Occasionally, in very heavy infections consisting of about fifty onchospheres, cavity-formation is delayed until the flea has nearly completed the pupal period, or until the adult stage is attained. In infections of usual size, ranging from a few to twenty onchospheres, the cavity appears shortly after the second day of the pupal period when the infection is ten to thirteen days old. The cavity is formed by a peripheral migration of cells, accompanied by an increase in the size of the onchosphere. During this period of development, as previously noted, the inner cells are not bound together. The intercellular fluid collects in this cavity and also increases in amount. The cavity is almost spheric when small (FIGURE 31), but as it increases in size the shape may become irregular. Sometimes the cavity is dumb-bell-shaped (FIGURE 32), and two cavities appear to be present due to the small size of the communications between the two portions. The dimensions of the cavity vary considerably. The maximum size is approximately two thirds the greatest diameter of the onchosphere. The boundary of the cavity consists of the surrounding cells, since the cavity does not have a definite lining, but is in communication with all the intercellular spaces; these, however, are not large at this time.

During this stage of development the onchosphere is fragile and disintegrates quickly after removal from the host. Within one minute after dissection out of the host, fluid begins to collect under the cuticula which becomes separated from the underlying cells and assumes a blistered appearance. As the blisters increase in number and in size (FIGURE 34) the cavity diminishes until it disappears. The entire process requires three to four minutes and at the end of five minutes disintegration is complete. This phenomenon has been observed in tap-water, distilled water, a series of salt solutions of varying concentrations, and albumen-water, with little change in the time required.

As the cavity becomes larger, it progressively approaches the anterior end of the onchosphere and is eventually located adjacent to the hooks (FIGURE 33). The shape of the onchosphere changes from spheric to ovoid, being slightly wider at the hook-bearing end (FIGURE 53). It is in this stage at the close of the pupal period.

The body of the onchosphere at this time consists almost entirely of germinative cells, similar in staining reactions to those of the preceding stage. These cells divide rapidly as the individual increases in size. They are closely approximated in the end opposite from the hooks, but are separated elsewhere by intercellular spaces. The cytoplasm is small in amount and in fixed material, as a result of shrinkage, it is rather difficult to demonstrate. During this period of rapid division the nuclei are smaller, and the proportion of cytoplasm to nuclear substance is less than formerly. A few larger cells, located at the periphery and mainly near the hooks, are germinative cells which have not recently divided. These cells, conspicuous because of their large size, appear to be in a degenerating condition. The nucleus is stained very lightly, and in some instances is difficult to demonstrate. The cytoplasm is vesicular and relatively large in amount. Other bodies, in addition to the nucleus, are enclosed by the cell-membrane. It is probable that these cells, which make their appearance when the cavity has reached maximum size, will contain the first calcareous corpuscles. A few germinative-somatic cells are scattered among the germinative cells.

The cuticular covering grows thicker by the addition of material to the inner surface, and in sections the older layers can be distinguished from the newer layers. The outermost layers are shed. Depositing and shedding of cuticula appear to be continuous processes. Fragments of old cuticula frequently adhere to the onchosphere and give it a rough and wrinkled aspect or the appearance of being enclosed in an envelope. The subcuticular cells are not arranged in any definite fashion and there is no morphological evidence that any particular type of cell is responsible for the secretion.

Metamorphosis of Onchosphere into Cysticercoid in the Adult Flea

When the infected flea emerges from the cocoon the ovoid onchospheres are located in the abdominal cavity. They are white, opaque, granular in appearance, and measure 50 by 85 microns. They can not move about, but an ovoid specimen 85 microns in length may contract into a sphere 60 microns in diameter or extend to a size of 40 by 140 microns. The hooks may be located superficially or embedded among the cells in the cortical region. Often one or both members of a pair are lacking and six hooks are present only in rare specimens. No cellular details can be seen in living specimens (FIGURE 54). Sections show that the larva consists principally of germinative cells; these are closer together in the cortical region than in the center (FIGURE 55),

but even in the cortical area large intercellular spaces may be present. A few cells, scattered throughout but mainly adjacent to the cuticula, are fusiform in shape and may be contractile in function. The large cells which will form calcareous corpuscles in their cytoplasm become common and are located particularly in the cortical layer (FIGURE 50). A few germinative-somatic cells are present. The cavity which formerly was prominent is filled with a spongy core of germinative cells; remnants of the cavity persist as intercellular spaces.

The first indication of the cysticercoid stage is evident in the onchosphere within a few days after emergence of the host. The portion to which the hooks are, or were, attached is delimited from the body as a tail-like appendage, the cercomer (FIGURE 38), which takes no share in formation of the cysticercoid. If the hooks remain, the median pair lies near the end of the cercomer and an antero-lateral pair on each side. An exception was observed in a cercomer with only one hook of an anterolateral pair remaining. In addition to its cuticular covering and all remaining hexacanth hooks, the cercomer consists of germinative cells in a degenerating state, liquid, and sometimes a few calcareous corpuscles.

During its formative period the shape of the cercomer varies with the form of the onchosphere. When the latter is spheric, the cercomer diminishes in size and may vanish, but otherwise it is a distinct and flexible appendage (FIGURES 36 to 38). As development proceeds the ability to change shape is lost to a large extent. Young cercomers retract when fixed (FIGURE 39) but older ones retain their shape (FIGURES 41 and 43). A constriction, appearing posterior to the lateral pairs of hooks and separating the cercomer from the body (FIGURE 40), deepens gradually until the connection between the two parts is very small. Approximately ten days are required for the cercomer to develop and then it is shed.

The polarity is reversed during the period in which the cercomer is formed. The end opposite from the cercomer becomes the anterior end because it now precedes the other end in locomotion. It must be remembered when this change occurs (FIGURE 40); otherwise, the terms *anterior* and *posterior* might cause confusion in the following description.

Shortly after the appearance of the cercomer (FIGURES 40 and 41), an anterior invagination develops and the cells below it divide rapidly to form a dense cluster which will give rise to the rostellum. Four invaginations in the cuticula, symmetrically arranged around the first invagination, indicate the positions in which the four suckers will

develop (FIGURE 42). The anterior end continues to invaginate until the rostellum and primordia of the suckers are located within the cystoid body of the cysticercoid (FIGURE 43). The rostellum develops first and it consists of a dense cylindric bundle of cells covered with cuticula armed with hooks. When the rostellum is fully formed, it is not in an inverted position, but has the same relationship to the cysticercoid as it has to the adult cestode (FIGURES 44 and 48). The suckers consist of dense masses of germinative cells. Their concave surfaces face toward the center of the cysticercoid and are covered with cuticula continuous with external covering. On all other surfaces, the sucker is delimited from the cells, in which it is supported, by a thin layer of cuticula. After development of the rostellum and suckers, which requires approximately eighteen days in the adult flea, the scolex may be forced into the definitive position by pressure of a coverglass. In this position the suckers have the cup-shaped appearance characteristic of the adult cestode.

The first evidence of an excretory system is a small cavity that develops in a posterior mass of germinative cells situated dorsal to the attachment of the cercomer. The cavity elongates longitudinally and makes contact with the cuticula at the posterior end where an outlet forms (FIGURE 57). The posterior part of this cavity later becomes the bladder. Anteriorly the cavity becomes divided into two dorsal and two ventral portions, which extend forward by intracellular extension (FIGURE 47) and form the excretory tubes. The tubes diminish in diameter towards the anterior end and form tubules which extend into the scolex where they branch and anastomose. The entire system is lined with a thin layer of cuticula. Flame-cells have not been observed except in the cysticercoid after the bladder and excretory tubules have appeared. Each flame-cell (FIGURE 49) develops from a germinative cell. The cilia are first evident as a rod-shaped structure which shows staining reactions similar to those of the nucleus, and either consists of fused cilia or subdivides into cilia. The flame-cells are joined to the main excretory ducts by a system of small tubules.

Ovoid and spheric calcareous bodies, measuring 3 to 10 microns, are numerous in the mature cysticercoid. They are distributed throughout the body, with the possible exception of the scolex, and are especially numerous in the region immediately anterior to the bladder. Intracellular bodies in the rostellum and suckers appear to be globules of fat in living specimens, and are represented by spaces in sectioned material (FIGURES 46 and 48).

Much of the interior of the cysticercoid is filled with parenchyma (FIGURE 57), which develops from germinative cells. The parenchymatous cells have irregular boundaries and long extensions which meet with similar processes from other cells. This tissue constitutes a foundation for the cuticula and supports the various internal organs.

Cysticercoids dissected from fleas approximately thirty days after infection have changed from spheric to pyriform shape; the scolex is then located in the wider end. The behavior of the cestode suggests a well developed muscular system, but the characteristic musculature of proglottids is not present. Some of the fibers amongst the parenchymatous cells have undulations similar to those in mature proglottids, and the movements must be caused by contraction of these fibers, even though they do not seem to be arranged in a definite system.

The interior of the cysticercoid consists of parenchyma, a few germinative-somatic and germinative cells, the structures previously described, and the nervous system which was not studied. The germinative cells occur throughout the body of the organism but are concentrated in the neck region of the scolex, which will grow rapidly to produce the segments of the adult cestode.

The cystoid body (FIGURE 44), which surrounds the scolex, develops into the first proglottid after ingestion by a definitive host. This segment, which contains the excretory bladder, does not grow as rapidly as the one to which it is attached, and usually drops off before the strobila attains a length of three centimeters.

Cysticercoids are infective for the definitive host after living approximately eighteen days in the adult flea or about thirty days after the flea larva was infected. The time may be as short as twenty-two days and as long as forty-eight. The length of time varies with factors previously mentioned.

The mature cysticercoid lies free in the abdominal cavity of the flea. When the abdomen of an infected flea is torn apart in a drop of salt solution the parasites float out into the surrounding fluid. They are white, slightly flattened dorso-ventrally, and measure about 250 to 300 microns when contracted (FIGURE 44) and 250 by 600 microns when extended (FIGURE 45).

Effects of the Cestode on the Intermediate Host

The cestode produces definite effects on the intermediate host. Observations on the extent of infection in relation to mortality of dog fleas is in agreement with the observations on cat fleas, recorded by Chen (1934). A large proportion of flea larvae die shortly after

infection. Some enter the prepupal stage, which involves cessation of feeding and evacuation of the intestinal contents, but do not attempt to spin a cocoon and wander about until they die. A few pupate without spinning cocoons and produce normal adults. Approximately twenty per cent of those in cocoons fail to emerge. About half of such cocoons contain dead pupae and the remainder contain adult fleas which appear normal and will live, even though they were unable to make their own way out of the cocoon. Normal adult fleas are positively phototropic, but heavily infected individuals often respond negatively to light. Additional reversed behavior is exhibited by a negative response to a host. Infected fleas frequently are sluggish in their movements, which renders them more susceptible to ingestion by a dog.

THE CYSTICERCOID IN THE DEFINITIVE HOST

A hiatus still exists in our knowledge concerning development of the tapeworm in the final host. Dogs and cats become infected when they are fed fleas which contain mature cysticercoids. Apparently the enzymes in a definitive host are capable of digesting fleas to a degree such that any cysticercoids, if present, are allowed to escape. The scolex of the liberated cysticercoid is everted and the larva becomes attached to the mucosa of the small intestine. Segments are budded off from the neck region of the scolex and produces a strobila. Growth of the tapeworm is influenced by the diet, age, and health of the host. Liquid foods, especially milk, are conducive to rapid growth. Repeated attempts to infect dogs in the initial coryza stage of distemper failed. Infected dogs that develop distemper lose their *Dipylidium* when gastro-intestinal disturbances appear.

The cestode grows more rapidly in the dog than in the cat. Cysticercoids of the same age, derived from the same proglottid, were fed to a dog and cat on the same day. Post-mortem examination of the cat twenty-three days later yielded several tapeworms, the longest of which measured 115 millimeters. The dog, examined two days later, contained tapeworms 250 millimeters in length. The cestodes from the cat were also more delicate in structure than those from the dog.

Dipylidium caninum does not produce ill effects in the dog unless it is present in large numbers. Diarrhea develops in dogs forty-eight to seventy-two hours after infection and subsides after a few days. A severe hemorrhagic enteritis is often associated with the presence of more than one hundred. The tapeworm becomes attached to the intestinal epithelium by the scolex which is usually inserted into a

gland opening. The scolex may penetrate into the submucosa, pulling the neck region and the immature segments after it. The enteritis is probably due to the burrowing habits, either directly, or perhaps indirectly due to a bacterial invasion. Proglottids crawling through the anus to the outside irritate most dogs and result in vigorous scratching of the afflicted part.

NORMAL VARIATION IN DIPYLIDIUM CANINUM

The following experiment, typical of several, was performed in order to determine the amount of normal variation in *D. caninum*. A typical adult specimen was selected from a freshly killed dog, and the posterior gravid segment was removed. The eggs were removed, concentrated, washed in Ringer's solution, and then fed to approximately 300 eight-day-old flea larvae. The fleas began to emerge from their cocoons eighteen days later. When the adult fleas were twenty days old, four of them, that appeared to carry heavy infections, were fed to a cat. The remaining ones were divided into approximately three equal groups and fed to three dogs in ground beef. The cat was sacrificed and examined after twenty-three days, and two of the dogs were examined two days later. The cat harbored thirty-one specimens; one dog had three and the other had fifteen. These worms were placed, one at a time, on a glass plate and fixed in a hot mixture of nine parts saturated aqueous solution of corrosive sublimate and one part of glacial acetic acid. They were then stained in borax carmine.

Twenty-two characters have been utilized as specific criteria in descriptions of new species; these are discussed below, with reference to observations on live material, whole mounts, and serial sections. Over 10,000 worms from dogs and cats have been examined in the past five years. In addition, special study was made of thirty-one specimens from a cat and eighteen specimens from two litter-mate mongrel puppies, which were infected with cysticercoids from eggs of one proglottid.

(1) *Total length and greatest width.* These are variable within wide limits. A fresh, contracted worm may be three times as long after it is relaxed and killed. If the worm is allowed to die before fixation, its length is always greater than if it had been fixed when alive. Specimens of the same age vary in length. Worms from the dog, which were twenty-five days old, measured 75 to 250 mm. in length. Although a single specimen becomes narrower as it elongates, in general the width of a strobila bears a close relation to its length, with the

greater width in the longer specimens. A live proglottid may change its width greatly and it can be fixed in either the wide or narrow condition. In tapeworms compressed between glass slides, during or after fixation, the natural variation may be greatly exaggerated.

(2) *Shape and size of the scolex.* In living worms this assumes a variety of shapes in rapid succession. Its shape in the killed worm depends upon its shape at the time of fixation. Designations such as ovoid, rhomboid, conic, cuboid, globular, club-shaped, etc., are worthless. The length of the scolex cannot be measured accurately in whole mounts, because there is no gross morphological demarcation between scolex and neck. The width of the scolex varies according to its shape; it is from 0.25 to 0.5 mm. in worms from experimental infections.

(3) *Shape and size of the suckers.* These are cup-shaped, muscular, adhesive organs, which vary from circular to elliptic on the same scolex. Their size varies greatly in living specimens, and from 0.11 to to 0.2 mm. in fixed ones.

(4) *Shape and size of the rostellum.* This consists of a dense bundle of cells covered with a heavy cuticula armed with hooks. It is a flexible, penetrating organ with a constantly changing shape in living specimens, and may be retracted or extended and rotated slightly. In preserved worms from experimental infections the length varies from 0.125 mm. to 0.175 mm.

(5) *Number of rows of hooks on the rostellum.* Baylis (1929, p. 100) states: "The hooks are usually described in terms of transverse rows. They are not, however, arranged in straight transverse rows, but appear rather to be alternating *longitudinal* rows having a tendency to run spirally round the rostellum. It is possible for different observers, or the same observer, to obtain varying results when attempting to count the 'transverse' rows in the same specimen. Still more is this the case with different specimens showing even the slightest individual variation either in the size and shape of the rostellum or in the total number of hooks." Witenberg (1932) described the hooks as arranged in alternating transverse rows, that is in quincuncial order. He determined the number of transverse rows by counting the hooks in a spiral course from the base to the tip of the rostellum. Utilizing this method, he always found four to seven rows on the rostellum of *D. caninum*. By using the same method of determination, one to seven rows may be counted on specimens with a common origin from eggs of the same proglottid. When only one or two rows are present the condition is atypical, and is the result of treatment the worm has received. Worms have been removed from

the intestine and the rows of hooks counted. These specimens were allowed to reattach to the mucosa and then forcibly removed. Occasionally the worm would break at the neck region, but if it did not, the rostellum would sometimes be stripped of many hooks. Worms allowed to stand in water or saline solution for several hours before fixation will lose hooks; some lose all of them after such treatment. In young worms the hooks form a more definite pattern than in older specimens, indicating that with increasing age hooks may be lost. It is therefore futile to attempt a fine distinction in the number of rows.

(6) *Size of the hooks.* The apical ones measure 0.004 mm.; the basal ones do not exceed 0.016 mm. All are shaped like rose thorns.

(7) *Length and width of the neck.* The junction of the neck to the scolex cannot be distinguished in whole mounts. In order to reduce the possible error I have always made the measurement from the anterior tip of the scolex to the anterior border of the first proglottid. If the neck is contracted it is broad and the borders are scalloped, so that the appearance of segments immediately adjacent to the neck is simulated. When the neck is extended the borders are smooth. In relaxed specimens from experimental infections the neck varies from 0.9 to 1.5 mm. in length.

(8) *Size of immature, mature, and gravid segments.* Variations in the dimensions of segments are always evident in the same strobila.

(9) *Total number of segments.* This varies according to the age of the worm, although the number may vary one hundred per cent in young worms of the same age. Proglottids containing egg-capsules may be produced in strobilas of fifty segments. In whole mounts these segments appear similar, except in size, to gravid proglottids from strobilas of one hundred and fifty or more segments. Proglottids from short strobilas are seldom if ever shed, their color is yellowish and the egg-capsules are gluey when teased from the proglottid; such eggs produce low-grade infections in flea larvae. Proglottids from long strobilas are shed regularly, as evidenced by daily fecal examination over a period of time followed by autopsy of the host, and they have a reddish color; the eggs from these proglottids are highly infective for flea larvae.

(10) *Lateral margins of proglottids.* Smooth, convex, or irregular lateral margins of the proglottids are correlated with relaxation or contraction of the worm.

(11) *Segment where genital primordia first appear.* In young worms this may occur in the tenth segment; in older worms they may not appear until the fiftieth segment. In young worms of the same age the variation is from segment ten to segment seventeen.

(12) *Position of genital sinus.* Always near or slightly posterior to the middle of the lateral border of the sexually mature segment. In sexually immature segments, the sinus may be slightly anterior to the middle of the proglottid.

(13) *Shape, length, and position of the cirrus-sac.* In worms from experimental infections the cirrus-sac is elliptic to pyriform, with a length of 0.2 to 0.3 millimeters. The cirrus-sac is usually lateral to the longitudinal excretory canal, but if the retractor fibers attached to its medial end are greatly contracted it may extend across the canal.

(14) *Size, number, and distribution of the testes.* These are 0.1 mm. or less in diameter. There are about two hundred of them distributed between the longitudinal excretory canals of sexually mature proglottids. The majority lie anterior to the female reproductive organs. The difference in numbers, apparent rather than real, is dependent upon the fixing and staining technique. Often some of them do not take the stain or are destained until scarcely visible; a testis which has shed its sperm takes a very light stain. It is probable, from casual observations on sectioned material, that all segments in the same stage of development have approximately the same number of testes.

(15) *Shape, size, and position of the ovary.* This is composed of numerous follicles and its size and shape are correlated with their compactness or looseness. In a contracted segment the ovary is compressed and ovoid with the long axis transverse to the long axis of the worm. In a relaxed segment the long axis of the ovary is parallel to the long axis of the worm. An ovary depleted of its ova is smaller and stains more lightly than one with many ova. The longest diameter of the ovary varies from 0.25 to 0.5 mm.

(16) *Shape and size of the vitellarium.* The yolk-gland is approximately circular in outline and varies in size in different segments of the same worm. In contracted segments it is adjacent to the ovary but in relaxed segments some distance posterior to it.

(17) *Size and shape of the shell-gland.* This often stains poorly and sometimes appears to be absent. Slight variations in size and shape appear in the same worm.

(18) *Presence or absence of a seminal receptacle.* This is a dilated portion of the vagina, and may be present or absent in specimens from experimental infections. If present it may be small and indistinct or larger and easily distinguishable. The study of sectioned material suggests that the size of the structure and its staining capacity are correlated with the amount of sperm it contains.

(19) *Course of the vagina.* In immature segments it is often coiled; in mature segments the coils are lacking, or present only in that portion near the genital sinus.

(20) *Size and number of eggs and distribution of capsules.* The egg varies from 0.035 to 0.06 mm. in diameter. A variation from 0.041 to 0.0603 mm. was noted in the eggs of a single capsule. Fresh eggs, not compressed, and eggs in sectioned material are always within the limits stated above. The onchosphere is 0.02 to 0.034 mm. in diameter; the larval hooks measure 0.0105 mm. in length. As many as sixty-three eggs were observed in a single capsule. The number of eggs per capsule is not constant even for a single proglottid, as may be observed in capsules teased from a fresh proglottid and studied under low magnification. The capsules occupy almost the entire area of a gravid proglottid between the longitudinal excretory canals, and occasionally, when many capsules are present, they may extend beyond the canals. The latter condition is most likely to occur in proglottids which are about to be detached. Compression of fresh material will cause the capsules to move about and occupy the entire interior of a proglottid.

(21) *Width and distinctness of the excretory canals.* These are narrow or wide according to whether they are empty or filled with fluid. They are very distinct in specimens greatly overstained and then rapidly destained.

(22) *Geographical distribution.* The hosts of this worm are cosmopolitan in distribution. There is interchange of hosts from region to region, permitting a cosmopolitan distribution for the parasite.

SPECIES OF DIPYLIDIUM

With a more definite knowledge of the normal variation of these characters, it is possible to evaluate the species that have been described. The following species in addition to the type (*D. caninum*) have been described and placed by their authors in the genus *Dipylidium.* They are arranged in chronological order.

Dipylidium oerleyi Rátz, 1900
Dipylidium sexcoronatum Rátz, 1900
Dipylidium walkeri Sondhi, 1923
Dipylidium buencaminoi Tubangui, 1925
Dipylidium halli Tubangui, 1925
Dipylidium compactum Millzner, 1926
Dipylidium crassum Millzner, 1926
Dipylidium diffusum Millzner, 1926

Dipylidium gracile Millzner, 1926
Dipylidium longulum Millzner, 1926
Dipylidium carracidoi López-Neyra, 1928
Dipylidium porimamillanum López-Neyra, 1928
Dipylidium catus Gulati, 1929
Dipylidium otocyonis Joyeux, Baer & Martin, 1936

In order to prevent confusion the following species, in addition to those in the above list, must be mentioned briefly. *Dipylidium genettae* (Gervais, 1847) is based upon a confusion of two species of different genera. *Dipylidium monticellii* Diamare (1893), is too inadequately described ever to be recognized. *Dipylidium gervaisi* Setti (1895), *Dipylidium columbae* Fuhrmann (1908), and *Dipylidium dongolense* Beddard (1913), which were considered as *Dipylidium* by Witenberg, must be eliminated from that genus on the basis of our present knowledge of their morphology.

The original description of *Dipylidium oerleyi* Rátz (1900), and the supplemental description by López-Neyra (1929), agree with the description for *D. caninum* excepting the size of the egg. The diameter of the egg, recorded as 0.025 mm., may refer to the size of the onchosphere. In all other respects the description agrees with specimens of *D. caninum* from an experimental infection in a cat. The type specimen is lost (Witenberg, 1932). This species must be considered identical with *D. caninum.*

The main characteristics upon which *Dipylidium sexcoronatum* Rátz (1900) was established are: rostellum with six rows of hooks; seminal receptacle present; ovary compact and almost spheric; vitellaria reniform and close to the ovary; neck, immature and mature segments irregularly scalloped; and the egg 0.021 mm. in diameter. Many supplemental descriptions vary but little from the original one. All characteristics given for this species are within the limits of variation for *D. caninum*. As in *D. oerleyi,* the size of the egg might refer to the diameter of the onchosphere, since in whole mounts, the yolk-shell is often not very noticeable. The description for *D. sexcoronatum* is based upon contracted specimens of *D. caninum* and it is not a valid species. According to Witenberg (1932) the type specimens are lost.

Dipylidium walkeri Sondhi (1923) has no distinguishing characteristics to separate it from *D. caninum,* other than the measurements of the cirrus-sac. However, the measurements given by Sondhi are erroneous, as Lewis (1927) has pointed out. *D. walkeri* is synonymous with *D. caninum.*

Dipylidium buencaminoi Tubangui (1925) was described from the dog in Manila, Philippine Islands. Three distinctive features appear in the description for this species. The entire length of the specimens, with mature and gravid proglottids, is not over 30 millimeters. The largest hooks on the rostellum are 0.007 mm. in length. The diameter of the egg is about 0.008 millimeters. Could the size of the egg be stated incorrectly? In all other respects the species is quite similar to *D. caninum.*

Tubangui (1925) described *Dipylidium halli* as a parasite of cats in Manila, Philippine Islands. The original description is rather meager. López-Neyra (1929) recorded this species from cats in Spain. He included a detailed description of the species. The description agrees with *D. caninum,* except for the presence of the cirrus-pouches across the longitudinal excretory canals. The size of the pouches agrees in both species. The cirrus-pouches may extend beyond the longitudinal excretory canals in mature proglottids of *D. caninum,* but this condition is not typical of each proglottid in a strobila and is frequently found in specimens which were compressed when killed and fixed. Because of the lack of unquestionable differences from *D. caninum, D. halli* must be considered a synonym of the former species.

Dipylidium compactum, Dipylidium crassum, Dipylidium diffusum, Dipylidium gracile, and *Dipylidium longulum* were described from the dog and cat, or both, in California by Millzner (1926). Lewis (1927) reported the presence of *D. crassum, D. gracile,* and *D. longulum* in Wales. The latter author records intraspecific differences which are as great as some of the interspecific differences upon which these species were established. The present study has shown the characteristics upon which these species are established have no specific value. The five species described by Millzner are identical with *D. caninum.*

López-Neyra (1928) described *Dipylidium porimamillanum* from the dog and cat and *Dipylidium carracidoi* from the cat. It is impossible to distinguish these species from each other or from *D. caninum* due to overlapping of characteristics. The length of the onchosphere hooks in *D. carracidoi* was recorded as 0.007 to 0.008 mm. The larval hooks of *D. caninum* are 0.0105 mm. in length with very little range in variation. The apparent discrepancy can be permitted since accurate measurements in the egg are difficult to make except under the most favorable conditions. Both of these species are identical with *D. caninum.*

The description of *Dipylidium catus* Gulati (1929) is very similar to the description of *D. halli* Tubangui (1925). This species was reported from cats in India The cirrus-pouch extends median to the longitudi-

nal excretory canal. Gulati states that the actual length of the cirrus-pouch is of more value than whether it crosses the excretory canal, but he fails to include this measurement for the species which he describes as new. The only distinctive feature is the size of the egg, from 0.014 to 0.02 mm. in diameter. Until a more detailed study of the egg is made including total size with the embryonic coverings, size of the onchosphere and length of the larval hooks, the description cannot be accepted as representing a new species.

Dipylidium otocyonis Joyeux, Baer & Martin (1936) is characterized as follows: The length of well relaxed specimens is 17 mm. and the maximum width is 4 millimeters. The posterior segments have the shape of "cucurbitins" which is characteristic for *Dipylidium*. The musculature is only slightly developed, giving the worm a transparent aspect. The scolex has a diameter of 0.4 mm.; the suckers 0.13 mm.; and the rostellum 0.16 millimeters. There are four rows of rose-thorn-shaped hooks. Each row contains about 14, 16, 20 and 26 hooks with a total of around 76. They measure: 0.042 mm. for the first row; 0.038 mm. for the second row; 0.026 mm. for the third row; and 0.015 mm. for the fourth row. There are about 230 testes, 0.08 mm. in diameter. The genital pores are situated at about the middle of the segment. The egg capsules have 7 to 30 eggs with an average of 16. The spherical eggs are 0.045 to 0.05 mm. in diameter with an embryo 0.02 mm. in diameter. The larval hooks have a length of 0.008 mm. Host, *Otocyon megalotis* Desn. Distribution, North Somaliland, Africa.

The three valid species of the genus *Dipylidium* can be separated by the following key:

Rostellar hooks less than 0.016 mm. in length.
  Eggs 0.035 to 0.06 mm. in diameter.................................*D. caninum.*
  Eggs 0.008 mm. in diameter.................................*D. buencaminoi.*
Rostellar hooks in four rows, those of the first three rows 0.042 to 0.026 mm.
  in length...*D. otocyonis.*

•CLASSIFICATION AND DIAGNOSIS OF THE ADULT WORM

The classification of *Dipylidium caninum* is as follows:

Class Cestoidea Rudolphi, 1808
  Subclass Cestoda Monticella, 1892
    Order Cyclophyllidea Braun, 1900
      Family Dilepididae Fuhrmann, 1907
        Subfamily Dipylidiinae Stiles, 1896
          Genus *Dipylidium* Leuckart, 1863
            Species *caninum* Linnaeus, 1758

GENERIC DIAGNOSIS:

Dipylidiinae: rostellum muscular, retractile and armed with rose-thorn-shaped hooks which appear to be arranged in transverse rows; testes numerous, occupying most of the area medial to the longitudinal excretory canals; vagina opening posterior to the cirrus in a genital sinus; genital sinuses lateral, slightly posterior to the middle of the sexually mature proglottid; uterus reticular in ripe segments; eggs aggregated into capsules by a uterine secretion. Type species, *Dipylidium caninum.* Adults parasitic in mammals; earlier stages in insects.

SPECIFIC DIAGNOSIS:

The scolex is 0.25 mm. to 0.5 mm. wide. The suckers are prominent and circular to oval in shape, and 0.11 mm. to 0.2 mm. in diameter. The rostellum may be ovoid, conic, or globular, retracted or extended; according to its shape, it may be from 0.1 to 0.13 mm. wide and from 0.125 to 0.185 mm. long. The rostellum bears 30 to 150 characteristic rose-thorn-shaped hooks. They are not arranged in a definite pattern and may appear to be in transverse rows or often they may be resolved into longitudinal rows; both conditions may be found in the same specimen. The number of rows varies from one to seven in the same or in different specimens. These wide variations may be explained by the normal loss of hooks due to accident, age, and treatment after removal from the host. The greatest length of the hooks is 0.004 to 0.016 mm. with the larger hooks more distal. The neck is as long as broad and scalloped when contracted; in relaxed specimens it is smooth and may be 0.15 mm. wide and 1.5 mm. long.

Genital primordia are evident in the tenth to the fiftieth segment; the variation is due to the age of the worm and to the depth of stain. The genital sinuses are lateral in position and at the middle, or slightly posterior to the middle, of the proglottid. The testes appear first. They may be 0.1 mm. in diameter when mature. There are about two hundred, uniformly distributed in the space between the longitudinal excretory canals. The cirrus-sac is pyriform to elliptic in shape, and is 0.15 to 0.3 mm. long in mature segments. The medial end inclines toward the anterior end of the proglottid, and usually reaches to but may extend beyond the longitudinal excretory canal. The vas deferens is coiled and medial to the excretory canal.

The vagina may be coiled. It opens posterior to the cirrus. The ovary is bilobed, being divided by the vagina, and consists of numerous follicles. It is finely or coarsely lobulate, deep or light when stained, and large or small, due to the compactness or looseness of the follicles.

The lateral lobe is slightly smaller than the medial lobe. The entire ovary may be reniform, ovoid, elliptic, or spheric and 0.25 to 0.5 mm. in diameter. The yolk-gland is posterior to the ovary; it is similar to, but smaller than, the lateral lobe of the ovary. A small shell-gland of variable shape and size is located between the yolk-gland and the ovary. The shell-gland, while always a distinct structure in sections, often is indistinct in whole mounts. In ripe proglottids the uterus is a reticular structure. The eggs vary from 0.035 to 0.06 mm. in diameter. The onchosphere is 0.02 to 0.03 mm. in diameter, with six hooks that measure 0.0105 mm. in length. From one to sixty-three eggs are aggregated in a capsule by a uterine secretion. The capsules occupy practically the entire interior of a gravid proglottid.

The length of mature specimens varies between 150 and 700 mm.; the greatest width is 3.2 mm. The entire strobila consists of 60 to 175 segments (Witenberg gives the upper limit as 250). The newly formed segments are indistinct and wider than long. Mature and gravid segments are longer than wide and have smooth, convex lateral surfaces if relaxed and irregular lateral surfaces if contracted.

DEFINITIVE HOSTS: dog, cat, related carnivores, and man.
INTERMEDIATE HOST: the dog flea; the cat flea, human flea, and dog biting louse are known to harbor the parasite.
GEOGRAPHICAL DISTRIBUTION: cosmopolitan.

DISCUSSION

A discussion of the embryonic coverings of cestodes is, unfortunately, handicapped by lack of a uniform terminology. Moniez (1881) described two coverings for the *Dipylidium* embryo, the vitelline membrane and the granular envelope. He believed that the vitelline membrane was formed by modification of the peripheral cytoplasm of the fertilized ovum, the remaining material of the ovum shrinking so that the vitelline membrane became the loose outermost covering of the mature egg. It is evident that the "vitelline membrane" of Moniez is, in the immature egg, the structure that I have called the "shell" (FIGURE 3); this is a deciduous secretion of the shell-gland and is not present in the mature egg. The covering on the mature egg, which Moniez called the "vitelline membrane," is what I have called the "yolk-shell" (FIGURE 13, *ys*). It is not present on the unsegmented ovum but is formed from macromeres during later development. I have called this covering the yolk-shell because particles of yolk and the yolk-cell nucleus contribute to its formation

and, since it is the more or less tough outer covering of the mature egg, it may be considered a shell. The "granular envelope" of Moniez is what I have called the layer of albuminous material. It is located between the yolk-shell and the embryophore. Between the granular envelope and the developing embryo, Moniez recognized a thin layer around the embryo which, he suggested, might be a secretion of the embryo. This layer was undoubtedly the embryophore (FIGURE 13, *em*), and we know it arises from a group of micromeres (FIGURE 8). Benham (1901) accepted the suggestion made by Moniez, and Chen (1934) stated that the embryophore is excreted by the embryo.

In *Dipylidium caninum* almost the entire body of the cysticercoid is formed from the germinative cells, which have a capacity for rapid division. The neck region of the cysticercoid, which is the place of proglottid formation, contains many of these cells. In *Diphyllobothrium latum* they are important in forming much of the body of the procercoid (Vogel, 1930). In *Archigetes*, according to Wisniewski (1930), these cells form gonads. The germinative-somatic cells of *Dipylidium* do not contribute significantly to the mass of the larva, although they may give rise to the cells which contain lime and fat. The evidence suggests that they are germinative cells in which the single, large nucleolus has fragmented. In *Archigetes*, this type of cell forms parenchyma. The fate of the somatic cells in the onchosphere varies in different cestodes. In *Diphyllobothrium* these cells do not multiply rapidly and later disappear. Vogel suggested that they might contribute to the formation of parenchyma and muscle-cells of the procercoid. In *Triaenophorus* these cells divide rapidly and fill much of the body of the onchosphere. The somatic cells of *Archigetes* become numerous and form much of the parenchyma. In *Dipylidium* the somatic cells degenerate within a few days after the onchosphere hatches.

During the early development of the onchosphere of *Dipylidium*, after five to ten days in the flea, a study of living and sectioned material suggests that portions of the body are syncytial. An examination of a photograph (FIGURE 51) shows this condition in a living larva. Two to five nuclei appear to be enclosed within a membrane. The syncytial appearance will have to be investigated in more detail before a definite statement can be made. This condition is temporary and probably correlated with the high rate of cell division at this time.

Refractive granules have been noticed in the early stages of many species of cestodes. These granules are minute in size and may be exceedingly numerous. The granules are distributed quite evenly

throughout the onchosphere of *Dipylidium caninum* and appear to be located only in the intercellular fluid. A few granules are present when the onchosphere hatches and they become more numerous until after the formation of the excretory system, when they gradually disappear. For this reason it is suggested that these granules are concerned with excretion. Rosen (1919) believed the granules were located inside of the cells of *Diphyllobothrium latum*, but Vogel could not convince himself that they were intracellular in the same species. The granules were most numerous in the vicinity of the flame-cells. In *Triaenophorus*, Michajlow described cells of two different sizes which contained granules.

The present investigation agrees in all major respects with the observations recorded by Grassi & Rovelli on the stages which occur in the adult flea. Two differences may be noted. In the writer's material, the excretory pore does not form as early as the lacuna primitiva stage, but develops after the primordia of the scolex have appeared. Grassi & Rovelli described muscle-cells in the cysticercoid which, they stated, were similar in morphology and arrangement to the muscle-cells of adult cestodes and trematodes. None of my sectioned cysticercoids show musculature similar to that of adult *Dipylidium* proglottids. However, contractile fibers are present as extensions of germinative cells and are similar to the contractile fibers of the proglottid. These fibers are not arranged in definite layers or bundles.

The effects of *Dipylidium caninum* on cat fleas were studied by Chen (1934), who was particularly interested in the cellular defensive reactions of the host. The onchospheres were often encapsulated and reduced to a mass of yellow pigment. According to Chen this pigment is eliminated from the flea by direct passage through the epithelium of the ventriculus into the lumen of the intestine. The periods and rates of mortality for dog fleas correspond with the observations of Chen. The rate of death is correlated with the size of the infection, which is governed by the number of eggs fed to the larvae and by the instar utilized for the experiment. Older larvae have larger mouthparts and ingest more eggs than younger larvae.

The cysticercoid of *Dipylidium caninum* has been classified as a *Cercocystis* and as a *Cryptocystis*. Melnikow, in his original description, made no reference to a cercomer. His material was from the louse, *Trichodectes canis*. Sonsino (1889) observed cysticercoids from the dog flea, and he did not find a cercomer. Grassi & Rovelli described a cercomer for the cysticercoids they studied from the dog flea. The classification of the cysticercoid has been confused on the

basis of these observations. The present study shows that a cercomer is present at an early stage, but is lost. The cercocystis stage is a transient part of development and the mature cysticercoid is a cryptocystis.

Cestodes are covered externally by a cuticula. The various theories concerning the origin of the cuticula have been reviewed by Pratt (1909). They are as follows: (1) The cuticula is formed from a secretion produced by the subcuticula which is considered to be of ectodermal origin (Blochmann); (2) It is formed from a secretion produced by the subcuticula which consists of unicellular glands derived from the parenchyma (Brandes); (3) It is a metamorphosed ectoderm (Wagener); and (4) It is formed from secretions of the parenchyma and may have embedded in it portions of parenchymatous cells (supported by various investigations, before and since 1909, and due to his support it may aptly be called Pratt's theory). Pratt's theory is supported by the observations on *Dipylidium* and there is no support for any of the other theories. The recent revival of Blochmann's theory by Fuhrmann (1930) is refuted by the identical evidence presented by Pratt many years ago. Modern textbooks perpetuate the errors of the older textbooks on the subject of cuticula formation in the parasitic flatworms.

Three suggestions have been advanced for designation of the anterior end of the adult cestode. They are: (1) The larval hooks of the onchosphere are anterior in position and this relationship carries over into the adult worm, hence the scolex is located on the posterior end; (2) The larval hooks of the onchosphere are posterior in position and this relationship persists so that the scolex of the adult is anterior in position (since there is no evidence that the hooks are posterior in position, this suggestion will not be considered further); and (3) The onchosphere hooks are anterior in position and during metamorphosis into the bladderworm, the polarity of the animal is reversed and the scolex is anterior in position.

There is some embryologic evidence that the scolex is on the posterior end. The onchosphere always travels over surfaces and penetrates its host with the hooks in advance. There is no question but that the hook-bearing portion represents the anterior end. The scolex develops in the end opposite from the hooks. Hence it may be considered as located on the posterior end. After the scolex develops, it is in front during locomotion, which is not in harmony with this theory.

Watson (1911) studied the monozoic cestode *Gyrocotyle* in which there is an acetabulum at one end and a rosette at the opposite extrem-

ity. After a study of the morphology and behavior of this worm, Watson believed that the acetabulum was anterior and the rosette posterior. The acetabular end is foremost during locomotion. On the basis of a study of the comparative morphology of adult flatworms, the rosette was homologized with the scolex. While the orientation of *Gyrocotyle* appears to be justified, the homology is not based upon clear evidence as will be shown later.

The orthodox view has been to consider the scolex as representing the anterior end, since it contains the main mass of nervous tissue. In addition it may be pointed out that the scolex represents the only permanent part of the cestode. The intestine of a host may be split and the movements of short immature specimens of *Dipylidium* noted. The scolex is foremost in locomotion and may be used to pull the cestode over the mucosa, or the worm may crawl with little or no aid from this structure. It is also the most motile part of the animal. Gravid detached segments move with the end which was nearer to the scolex in advance. The scanty evidence from the few observations on cestode behavior indicates that the scolex is the anterior end of the worm.

Fuhrmann (1930) has supported the orthodox view. He, like Miss Watson, homologized the scolex with the rosette, but he believed that both are anterior in position. Concerning the orientation of the cestodes, he stated (page 400) "Was aber die ganze Frage der Orientierung entscheidet, ist der Umstand, dass die Lycophora (der *Cestodaria*) die sicher der Oncosphaera (der *Cestoda*) entspricht, an dem den Embryonalhaken gegenüberstehenden Pole bereits die Anlage eines Gehirns und besonders die für *alle Platoda* charakteristischen grossen Kopfdrüsen zeigt." He believed the rosette developed in the end opposite from the larval hooks. On this basis, the rosette was homologous to the scolex, since the latter structure also develops opposite from the hooks. Ruszkowski (1932) studied the lycophora and the evidence, which agrees with Fuhrmann's orientation of the larva, indicates that the hooks are posterior in position. Furthermore, he has shown that the rosette develops on the hook bearing end, hence this structure is posterior in position. Because of this fact, the homology of the rosette with the scolex is no longer tenable. Instead, the scolex should be compared with the acetabulum. Both structures develop in the end opposite from the hooks. These comparisons between the Monozoa and the Merozoa have yielded little information on the problem under consideration.

The onchosphere corresponds to the larvae of other animals. When a larval form is capable of locomotion, which is usually the case, and the adult form is sessile, a reorganization involving a change in the primary axis of the larva often takes place during metamorphosis. It seems logical to believe that the same phenomenon might occur in the cestodes. The following paragraph contains evidence to support this contention.

Essex (1928) studied two species of cestodes and recorded the following observations, "A shifting of polarity was noted in the course of the development of the larvae of both species of *Corallobothrium*. During their earlier phases (from the oncosphere to about ten days), when removed from the *Cyclops* they moved slowly about with the end bearing the hooks directed anteriorly. Coincident with the differentiation of the scolex at the opposite pole, their polarity was reversed and movements thereafter were made with the scolex-end in advance. This phenomenon was noted also by Janicki & Rosen (1918) in their study of *Diphyllobothrium latum*." Referring to Vogel's observations on *Diphyllobothrium latum*, Stunkard (1934) stated, "In this study Vogel has shown an actual metamorphosis between the onchosphere and procercoid stages, a reorganization which involves not only the cellular elements but also the antero-posterior axis of the larva. The anterior part of the onchosphere becomes the posterior end of the procercoid and vestiges of the onchosphere together with its hooks are cut off in the degenerating cercomere." The observations on *Dipylidium* which have been presented in this paper are in agreement with these descriptions.

SUMMARY

The literature on the larval and adult stages of the dog and cat tapeworm, *Dipylidium caninum*, is reviewed. A method is described by which the life-cycle was completed under experimental conditions. Observations on the morphology and bionomics of the larval and adult stages are given. Data on normal variation in adults developed from the eggs of a single gravid proglottid form the basis for a diagnostic description of *D. caninum* and permit an evaluation of the species that have been described for this genus. Three species are accepted as valid. Pratt's theory of cuticula formation is supported. The problem of orientation in the Cestoda is discussed

LIST OF REFERENCES

Baylis, Harry Arnold

1929. A manual of helminthology, medical and veterinary. i–ix. 1–303. 1929.

Beddard, Frank Evers

1913. Contributions to the anatomy and systematic arrangement of the Cestoidea. XI. On two species of tapeworms from *Genetta dongolana.* Proc. Zool. Soc. London 1913: 549–571. 1 S 1913.

Benham, William Blaxland

1901. The Platyhelmia, Mesozoa, and Nemertini. i–viii. 1–204. 1901. [Part 4 of a treatise on zoology edited by Edwin Ray Lankester. Cestoidea on pages 93–147.]

Brandt, Eduard Karlovič

1888. Zwei Fälle von *Taenia cucumerina* Rud. beim Menschen. Zool. Anz. 11: 481–484. 3 S 1888.

Brumpt, Émile Josef Alexandre

1926. Enkystement d'un anneau de *Dipylidium caninum* (L.) dans la paroi du gros intestin d'un jeune chat dysenterique. Arch. Schiffs-Hyg. 30: 365–368. 13 S 1926.

Campbell, Delwin Morton; & Lacroix, John Victor

1907. Essentials of parasitology, including a brief discourse on zoology. 1–96. *pl. 1–3.* 1907.

Chen, Hsin Tao

1934. Reactions of *Ctenocephalides felis* to *Dipylidium caninum.* Zeitschr. Paras. 6: 603–637. 2 Jl 1934.

Diamare, Vincenzo

1893. Il genere *Dipylidium* Lt. Atti Accad. Sci. Napoli II. 16^7: 1–31, *pl. 1–3.* 30 Je 1893.

Essex, Hiram Eli

1928. The structure and development of *Corallobothrium,* with descriptions of two new fish tapeworms. Univ. Illinois Biol. Monogr. 11: 255–328. *pl. 1–5.* 17 N 1928.

Fuhrmann, Otto

1908. Nouveaux ténias d'oiseaux. Rev. Suisse Zool. 16: 27–73. 1908.

1930–1931. Dritte Klasse des Cladus Plathelminthes: Cestoidea. Kükenthal & Krumbach, Handbuch der Zoologie. 2^2: 141–256. 18 Ja 1930; 257–416. 1 Ap 1931.

1935. Rectification de nomenclature. Ann. Paras. 13: 386. 1 Jl 1935.

Galli-Valerio, Bruno

1911. Notes de parasitologie et de technique parasitologique. Centr. Bakt. I. Abt. 60: 358–363. 7 O 1911.

Gervais, François Louis Paul

1847. Sur quelques Entozoaires taenioïdes et hydatides. Mém. Sci. Acad. Montpellier 1: 85–104. *pl. 1, 2.* 1847.

Grassi, Giovanni Battista

1888a. La pulce del cane (*Pulex serraticeps* Gervais) è l'ordinario ospite intermedio della *Taenia cucumerina.*—Nota preventiva. Bull. Soc. Entom. Ital. 20: 66. 1888.

1888b. Beiträge zur Kenntniss des Entwicklungscyclus von fünf Parasiten des Hundes (*Taenia cucumerina* Goeze; *Ascaris marginata* Rud.; *Spiroptera sanguinolenta* Rud.; *Filaria immitis* Leidy; und *Haematozoon* Lewis). Centr. Bakt. 4: 609–620. N 1888.

Grassi, Giovanni Battisa; & Rovelli, Giuseppe

1889a. Embryologische Forschungen an Cestoden. Centr. Bakt. 5: 370–377. 8 Mr 1889.

1889b. Embryologische Forschungen an Cestoden. (Schluss.) Centr. Bakt. 5: 401–410. 15 Mr 1889.

1892. Ricerche embriologische sui Cestodi. Atti Accad. Gioenia IV. 4^2: 1–109. *pl. 1–4.* 1892.

Gulati, Amar Nath

1929. Description of a new species of tapeworm, *Dipylidium catus* n. sp., with a note on the genus *Dipylidium* Leuckart, 1863. Bull. Agr. Res. Inst. Pusa 190: 1–14. 1929.

Henry & Leblois

1923. Cestodes, glandes anales et "maladie" des chiens. Recueil Méd. Vet. 99: 88–90. 15 F 1923.

Janicki, Constantin; & Rosen, Félix

1918. Le cycle évolutif du *Dibothryocephalus latus.* Récherches expérimentales et observations. Bull. Soc. Neuchât. Sci. Nat. 42: 19–53. 1918.

Joyeux, Charles Édouard

1916. Sur le cycle évolutif de quelques Cestodes. Note préliminaire. Bull. Soc. Path. Exot. 9: 578–583. [N] 1916.

1920. Cycle évolutif de quelques Cestodes. Bull. Biol. France 1920: Suppl. 2: 1–219. 1920.

Joyeux, Charles Édouard; Baer, Jean Georges; & Martin, R.

1936. Sur quelques Cestodes de la Somalie-Nord. Bull. Soc. Path. Exot. 29: 82–96. 1936.

Leuckart, Carl Georg Friedrich Rudolf

1863. Die menschlichen Parasiten und die von ihnen herrührenden Krankheiten 1: i–viii. 1–766. 1863.

Lewis, Edward Aneurin

1927. A study of the helminths of dogs and cats of Aberystwyth, Wales. Jour. Helminth. 5: 171–182. D 1927.

López-Neyra, Carlos Rodríguez y

1928. Recherches sur le genre *Dipylidium*, avec description de quatre espèces nouvelles. Bull. Soc. Path. Exot. 21: 239–253. [Ap] 1928.

1929. Revisión del género *Dipylidium* Leuckart. Mem. Acad. Cien. Madrid I. 32: 1–112. *pl. 1–24.* 1929.

Melnikow, Nikolai Fedorovič

1869. Ueber die Jugendzustande der *Taenia cucumerina.* Arch. Nat. 35^1: 62–69. 1869.

Michajlow, W.

1933. Les stades larvaires de *Triaenophorus nodulosus* (Pall.) 1. Le coracidium. Ann. Paras. 11: 339–358. 1 S 1933.

Millzner, Theresa Marie

1926. On the cestode genus *Dipylidium* from cats and dogs. Univ. Calif. Publ. Zool. 28: 317–356. *pl. 33–39.* 26 F 1926.

Moniez, Romain Louis

1880. Essai monographique sur les Cysticerques. Trav. Inst. Zool. Lille 3^1: 1–190. *pl. 1–3.* 1880.

1881. Mémoires sur les Cestodes. Trav. Inst. Zool. Lille 3^2: 1–238. *pl. 1–12.* 1881.

Pratt, Henry Sherring

1909. The cuticula and subcuticula of trematodes and cestodes. Am. Nat. 43: 705–720. D 1909.

Railliet, Alcide Louis Joseph

1892. Notices parasitologiques. Bull. Soc. Zool. France 17: 110–117. My 1892.

Ransom, Brayton Howard

1909. The taenioid cestodes of North American birds. U. S. Nat. Mus. Bull. 69: 1–141. 31 D 1909.

Rosen, Félix

1919. Recherches sur le développement des Cestodes. 1. Le cycle évolutif des Bothriocéphales. Bull. Soc. Neuchâtel. Sci. Nat. 43: 241–300. 1919.

Ruszkowski, Jerzy Stanisław

1932. Etude sur le cycle évolutif et sur la structure des Cestodes de mer. II ième partie. Sur les larves de *Gyrocotyle urna* (Gret Wagen). Bull. Int. Acad. Polon. 1931 (B2): 629–641. *pl. 41.* 1932.

Schiefferdecker, Ernst Friedrich Paul

1875. Ueber eine eigentümliche pathologische Veränderungen der Darmschleimhaut des Hundes durch *Taenia cucumerina.* Arch. Path. Anat. 62: 475–487. *pl. 8.* 15 F 1875.

Schwartz, Benjamin

1927. [The species of *Dipylidium* parasitic in dogs and cats in the United States.] Jour. Paras. 14: 68, 69. 26 O 1927.

Setti, Ernesto

1895. *Dipylidium gervaisi* n. sp., e qualche considerazione sui limiti specifici nei cestodi. Atti Soc. Ligust. 6: 99–106. *pl. 5.* 1895.

Sonsino, Prospero

1889. Ricerche sugli ematozoi del cane e sul ciclo vitale della *Tenia cucumerina.* Atti Soc. Tosc. Sci. Nat. Mem. 10: 20–65. *pl. 2.* 1889.

Steudener, Friedrich

1877. Untersuchungen über den feineren Bau der Cestoden. Abh. Nat. Ges. Halle 13: 277–316. *pl. 28–31*. 1877.

Stiles, Charles Wardell

1896. Report upon the present knowledge of the tape-worms of poultry. Bull. U. S. Dep. Agr. Animal Ind. 12: 9–79. *pl. 1–21*. 11 Jl 1896.

Stunkard, Horace Wesley

1934. Studies on the life-history of anoplocephaline cestodes. Zeitschr. Paras. 6: 481–507. 5 My 1934.

Tubangui, Marcos Angeles

1925. Metazoan parasites of Philippine domesticated animals. Phillip. Jour. Sci. 28: 11–37. *pl. 1–3*. 21 S 1925.

Venard, Carl Ernest; & Ellis, Percy Lester

1933. On cestodes from dogs. Veterinary Alumni Quart. (Ohio State Univ.) 21: 20–23. 1933.

Villot, Alfred

1882. L'appareil vasculaire des Trématodes, considéré sous le double point de vue de sa structure et de ses fonctions. Zool. Anz. 5: 505–508. 25 S 1882.

Vogel, Hans

1929. Studien zur Entwicklung von *Diphyllobothrium*. 1 Teil: Die Wimperlarvae von *Diphyllobothrium latum*. Zeitschr. Paras. 2: 213–222. 12 O 1929.

1930. Studien über die Entwicklung von *Diphyllobothrium*. II. Teil: Die Entwicklung des Procercoids von *Diphyllobothrium latum*. Zeitschr. Paras. 2: 629–644. 9 Au 1930.

Vogelsang, E. G.

1922. *Dipylidium caninum* en la vesicula bilar de un canino. Rev. Med. Vet. Móntevid. 31 D 1922.

Watson, Edna Earl

1911. The genus *Gyrocotyle*, and its significance for problems of cestode structure and phylogeny. Univ. Calif. Publ. Zool. 6: 353–468. *pl. 33–48*. 17 Je 1911.

Wisniewski, L. Wincenty

1930. Das Genus *Archigetes* R. Leuck. Eine Studie zur Anatomie, Histogenese, Systematik und Biologie. Mém. Acad. Polon. III. B2: 1–160. *pl. 1–8*. 1930.

Witenberg, George

1932. On the cestode subfamily Dipylidiinae Stiles. Zeitschr. Paras. 4: 542–584. 18 My 1932.

Young, Robert Thompson

1923. Gametogenesis in cestodes. Arch. Zellforsch. 17: 419-437. *pl. 17–20*. 4 D 1923.

Zschokke, Fritz

1903. Ein neuer Fall von *Dipylidium caninum* (L.) beim Menschen. Centr. Bakt. I. Abt. 34: 42, 43. 30 My 1903.

EXPLANATION OF FIGURES

FIGURES 1 to 12, 14, 15, 35, 39, 40, 41, 43, 44, 46 to 50, 53, 55, 56 and 57 are from permanent preparations; the remainder are from living material. With the exception of FIGURES 16, 17, 20 to 24, and 34, a camera lucida or other aids to drawing were utilized for FIGURES 1 to 50. FIGURES 51 to 57 are photomicrographs. Key to abbreviations: *em*, embryophore; *ys*, yolk-shell; *am*, albuminous material.

1. Mature ovum. × 1000.
2. Fertilized ovum showing a portion of the sperm. × 1000.
3. Fertilized ovum enclosed in the true shell. The ovum was still in the shell-gland. × 1000.
4. Two-blastomere stage. The yolk-cell nucleus is located above the blastomeres. × 750.
5. Three-blastomere stage. The true shell has loosened and become thinner. × 750.
6. Further stage in segmentation. The four macromeres and yolk-cell nucleus will form the yolk-shell; the micromeres will form the embryophore and embryo. × 750.
7. Yolk-cell. × 1000.
8. Stage showing formation of the embryophore. × 625.
9. Somatic cells of the onchosphere. × 1500.
10. Germinative cells of the onchosphere. × 1500.
11. Germinative-somatic cells of the onchosphere. × 1500.
12. Egg fixed in Gilson's fluid and stained with borax carmine. × 500.
13. Fresh egg from a gravid proglottid. × 500.
14. Section through a mature onchosphere showing the cells, cuticular covering of the embryo, embryophore, albuminous layer, and yolk-shell. × 1000.
15. Hatching of the embryo. Note that the hooks have no definite orientation to the ruptured coverings. × 500.
16. Onchosphere inside the embryophore and outside the yolk-shell; from the intestine of a flea larva. × 500.
17. Onchosphere hatched on a slide by pressure of a coverslip. × 500.
18. Egg-capsule containing three eggs. × 200.
19. Hexacanth hook. × 1500.

20, 21, 22, 23, and 24. Successive changes in bodily outline and hook positions during progression. × 625.

25. Onchosphere immediately after hatching. × 750.
26. Newly hatched onchosphere slightly compressed. × 750.
27. Onchosphere, five days old, from a flea larva. × 750.
28. Onchosphere, seven days after infection. × 625.
29. Dorsal aspect of ten-day-old onchosphere. × 750.
30. Ventral aspect of the specimen in FIGURE 29.

31, 32 and 33. Onchospheres from a flea pupa showing the lacuna primitiva. × 250.

34. Onchosphere in the lacuna primitiva stage several minutes after removal from the flea pupa. The liquid from the cavity has collected underneath the cuticula. × 250.
35. Onchosphere from an adult flea. × 250.

36, 37, and 38. Three views of the same onchosphere at the time the cercomer begins to form. × 250.

39. Onchosphere in which fixation caused retraction of the developing cercomer. × 250.

40. Cysticercoid in the stage where the polarity of the antero-posterior axis is reversed. × 250.

41. Stage slightly advanced over FIGURE 40. × 200.

42. Young cysticercoid, showing rostellum and sucker primordia. × 80.

43. Rostellar hooks beginning to form; cercomer fully developed. × 80.

44. Fully developed cysticercoid. × 80.

45. Cysticercoid with scolex evaginated by pressure applied to the larva. × 50.

46. Portion of a sucker. Note the large cells, which appear in the living condition to be filled with oil or fat. × 750.

47. Portion of the germinative cells showing the intracellular position of an excretory tubule. × 1000.

48. Section through the developing rostellum. × 500.

49. Flame-cell. × 1000.

50. Section of onchosphere five days after the flea host had become an adult. The cavity in the onchosphere had just disappeared. × 750.

51. Onchosphere from a flea larva ten days after infection.

52. Onchosphere from a flea larva seven days after infection.

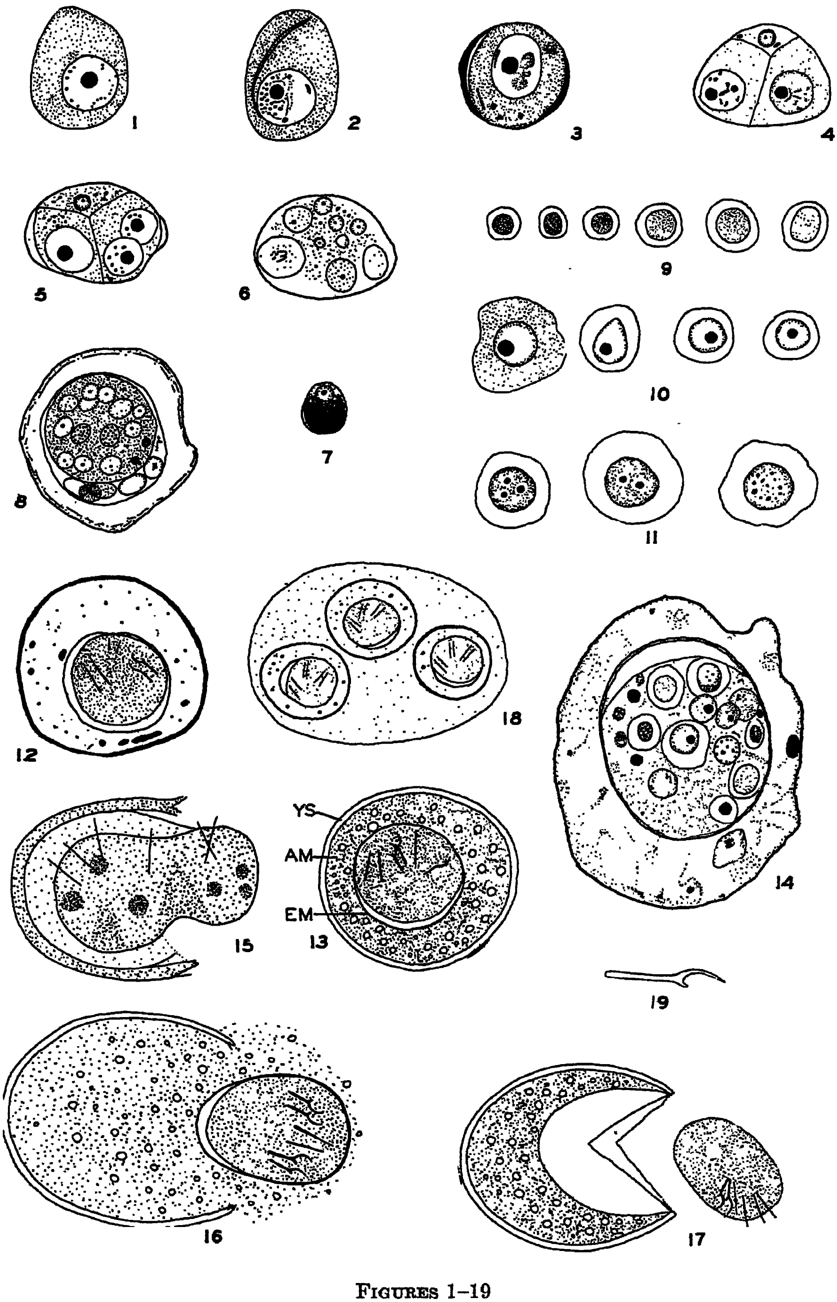
53. Section through a flea pupa showing two onchospheres in the cavity stage.

54. Onchosphere from a newly emerged adult flea.

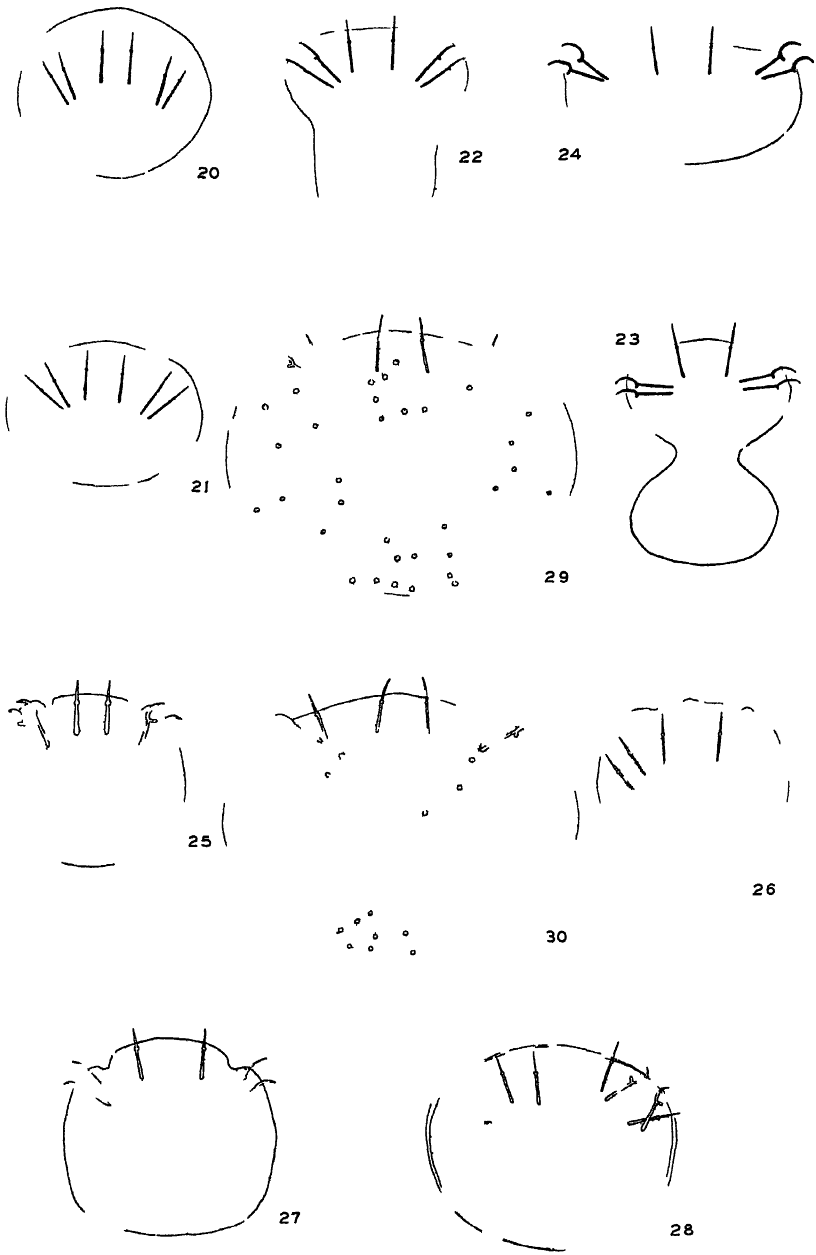
55. Cross-section of an onchosphere in stage represented in FIGURE 54.

56. Longitudinal section through a developing cysticercoid.

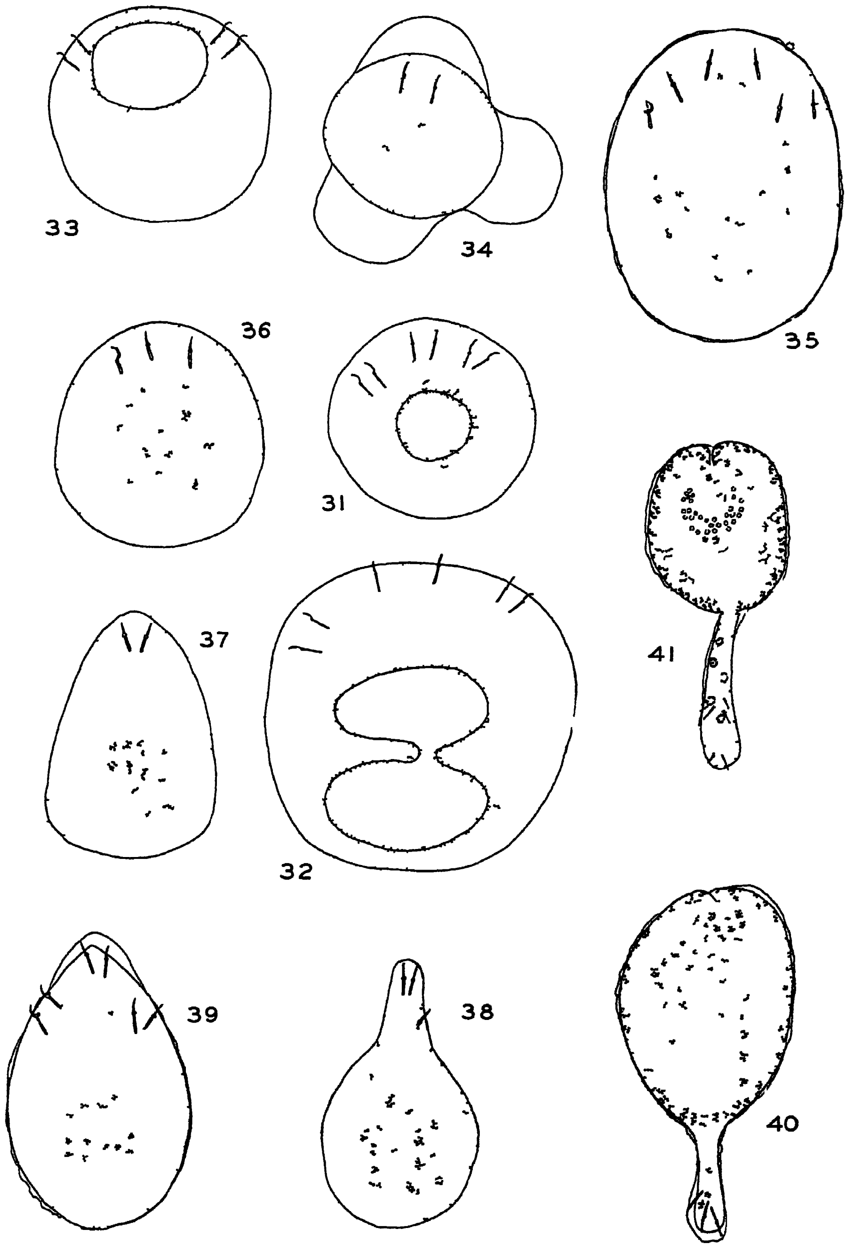
57. Section of a cysticercoid showing the cells and a portion of the excretory bladder.



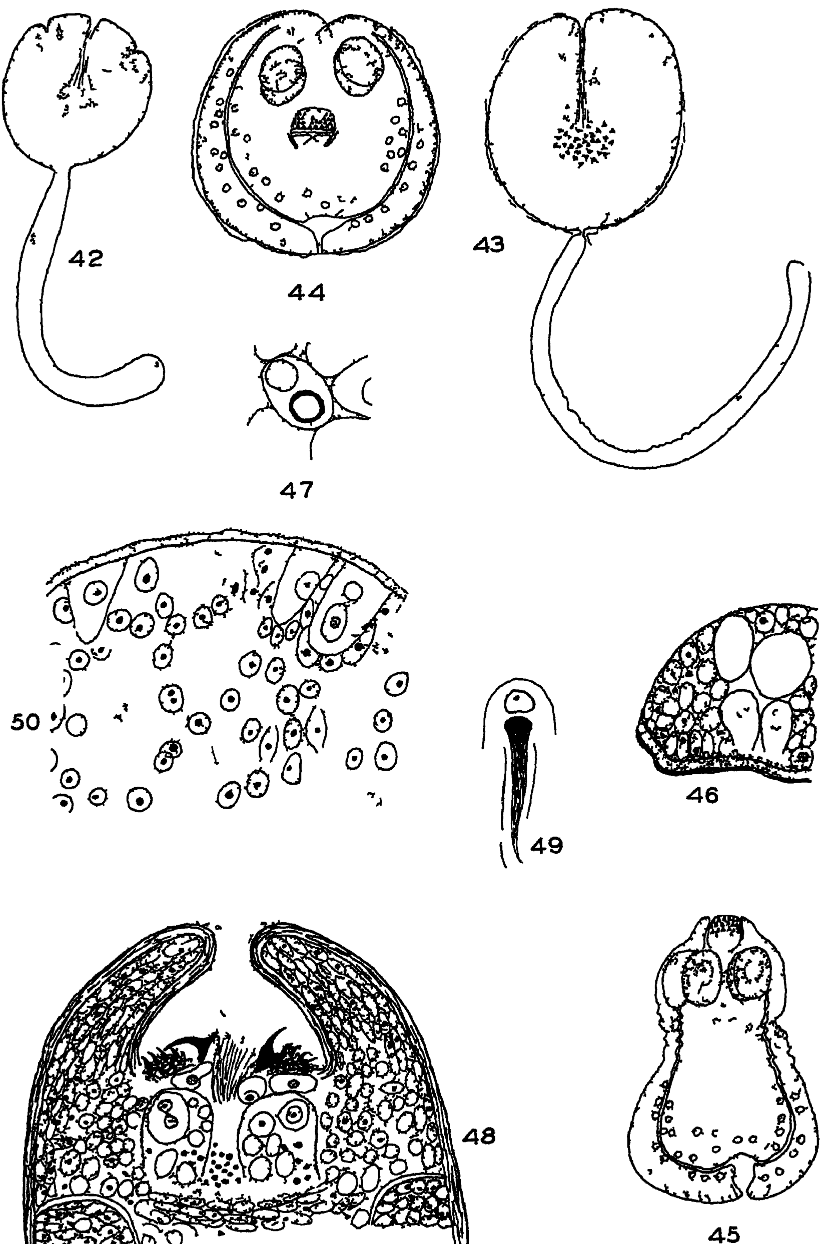
FIGURES 1–19



FIGURES 20–30



FIGURES 31–41



Figures 42-50

FIGURES 51–57

INDEX

ANNALS

OF THE

NEW YORK ACADEMY OF SCIENCES

VOLUME XXXVIII

NEW YORK
PUBLISHED BY THE ACADEMY
1939

Editor

JOHN HENDLEY BARNHART

Associate Editor

ERICH MAREN SCHLAIKJER

CONTENTS OF VOLUME XXXVIII

DATES OF PUBLICATION AND EDITION

Pp. 1–246, 4 January, 1939 1600 copies

Annals of the New York Academy of Sciences
Volume XXXVIII, pages 1–246, plates 1–22
January, 1939

MOLLUSCAN FAUNAS OF THE DOMENGINE AND ARROYO HONDO FORMATIONS OF THE CALIFORNIA EOCENE*

By Harold Ernest Vokes

CONTENTS

* Awarded an Honorable Mention in the New York Academy of Sciences A. Cressy Morrison Prize Competition in natural science for 1937. Publication made possible through grants from the income of the Ralph Winfred Tower Memorial Fund and the Esther Herrman Research Fund.

ACKNOWLEDGEMENTS

This study was made under the direction of Dr. B. L. Clark, to whom the writer is indebted for constant encouragement and helpful criticism both in the laboratory and in the field. Dr. R. W. Chaney of the Department of Paleontology, Dr. S. F. Light of the Department of Zoology, and Dr. C. D. Hulin of the Department of Geology of the University of California have always freely cooperated in problems connected with their fields of study. I am also indebted to Dr. H. G. Schenck of Stanford University for many helpful suggestions, and to Dr. L. G. Hertlein of the California Academy of Sciences for free access to its type collections. Dr. P. D. Trask of the United States Geological Survey offered invaluable suggestions in the field, aiding greatly in the solution of some of the problems in sedimentation. The writer's associates at the University of California, Dr. C. W. Merriam, Dr. F. E. Turner, Dr. R. A. Bramkamp, Mr. W. L. Effinger, and Mr. S. A. Berthiaume have assisted with much helpful discussion and suggestion in taxonomic problems.

Aid in the field has been freely given by Miss H. C. Lillis, Mr. Daniel McDonald, and Mr. William Ashurst. Mr. Lloyd Jones' hospitality during portions of two summers in the Vallecitos area has had much to do with the success of the work.

The constant helpful and understanding encouragement of the writer's wife has had no small part in the completion of this study, and the drawings of the hinges of the Pelecypoda, here included, are to be credited to her.

INTRODUCTION

The value of the deposits of petroleum occurring along the western margin of the San Joaquin Valley has resulted in many detailed geologic studies of this area; consequently, the stratigraphy is well known. The faunas have not received a commensurate amount of attention and, while their broad features are known, the details have not as yet been investigated. It is the purpose of this paper to record the faunas and the faunal sequence of the Eocene horizons which are exposed in the Vallecitos and Coalinga areas along the western border of the San Joaquin Valley, California. Emphasis has been placed upon the study of the fauna of the Domengine formation, the type section of which occurs north of Coalinga on the Domengine Ranch, since it is thought that a knowledge and understanding of this fauna is of supreme importance in the use of this horizon as a faunal unit throughout the West Coast Tertiary sequence. The study of the fauna of the Capay stage as represented at Coalinga has been considered of secondary importance, and the main efforts have been directed toward the understanding of the relationship of this fauna to that of the Domengine formation. Stratigraphic problems have been considered only as they apply to an understanding of the faunal problems involved.

HISTORICAL REVIEW

The economic importance of the Coalinga region has resulted in the publication of a large number of papers. In many of these the Eocene strata are mentioned only incidentally. The following review has been limited to those studies which are significant in the development of the present age-concept of the horizons represented, or in which contributions are made to the knowledge of the faunas.

The first record of the occurrence of Eocene strata in the area studied was given by Whitney in 1865 (57). In discussing a trip made with Gabb to New Idria, he says:

> The New Idria furnace or 'hacienda' is situated just within the borders of the metamorphic. . . . From specimens obtained a few miles east of the furnace Mr. Gabb was inclined to the belief that the Eocene period of the Tertiary was there represented; if so it would be the only locality in this state where this formation has been detected.

Later study apparently caused Gabb to change his opinion concerning the Eocene age of these strata, and in the second volume of the "Paleontology of California" (1869) the fossils were referred to the Tejon Group, Division B of the Cretaceous. The new species which were described from the Vallecitos were:

Ostrea idriaensis	*Neverita globosa*
Donax lata	*Loxotrema turrita*
*Pecten interradiatus**	*Nerita (Theliostyla) triangulata*

In the preface to this publication Whitney (1869: xiii) states:

> The Tejon Group, the most modern member, the Division B of Paleontology, Vol. I, is peculiar to California. . . . It was discovered . . . in the Coast Ranges . . . as far south as New Idria. . . . Mr. Gabb considers it as the probable equivalent of the Maestricht beds of Europe.

The next publications upon this region were those of White (1885, 1889) and Becker (1888, 1889). Becker's conclusions regarding the Eocene deposits are summarized as follows (1889: 977):

> The Chico and Tejon are absolutely conformable at New Idria and sedimentation went on continuously from one period to the other. Fossils are not numerous, but are present in sufficient number fully to identify the age of the rocks.

This view was concurred in by White, who considered that the Chico horizon represented the Uppermost Cretaceous and the Tejon the Lower Tertiary of the West Coast. In 1889 (20) he described *Rimella macilenta* from the "Chico Group, about 2 miles northward from New Idria, Fresno County."

This concept of continuous sedimentation between the Cretaceous and the Tertiary in the New Idria region led to further study by Turner & Stanton (1894) and by Stanton (1896), who concurred in recognizing the "apparently conformable" nature of the two series. Stanton showed (1896: 1027) that the Chico fauna occurred at the base of the section and the Tejon fauna at the top, with a thick series of unfossiliferous beds between. The Tejon fauna was recognized as equivalent to the upper beds at Mount Diablo. Concerning the apparent conformity of the strata within the series he concludes (1035): "So far as it goes this is an indication of continuous sedimentation, but without further evidence it cannot be accepted as proof that there is no break."

* This species occurs only in the white and brown siliceous shales at the base of the Kreyenhagen formation and is probably of Upper Eocene or Lower Oligocene age.

Just two years previously Watts (1894) gave the first record of the occurrence of Eocene strata at the coal mines northwest of Coalinga. The fossils collected were determined by Cooper and, due to a number of misidentifications, the age-relationships were somewhat obscured; Cooper concluded that they were somewhat intermediate in age between the Cretaceous A (true Cretaceous) and Cretaceous B (Eocene) of Gabb, and were stratigraphically lower than the coal mines near Mount Diablo. During the same year Cooper (1894) described *Cerithidea carbonicola* and *Mytilus dichotomus* from the "headwall of the California Coal Mine, near Huron, Fresno County," and in 1896 he described *Sigaretus costatus* and *Calliostoma lignitica* from the San Joaquin Coal Mine.

Eldridge in 1903 (307) mentioned the occurrence of Tejon sands in the Coalinga Oil Field, the first definite reference of these Coalinga strata to that horizon.

F. M. Anderson's "Stratigraphic study in the Mount Diablo Range of California" (1905) represents the first detailed stratigraphic study attempted within this area. Three new molluscan species, *Spondylus carlosensis, Ostrea aviculiformis,* and *Cypraea fresnoensis* were described from the Eocene deposits. Along Reef Ridge, south of Coalinga, two lithologic members were recognized in the Tejon: a lower sand named the Avenal sand and an upper shale, the Kreyenhagen shale. North of Coalinga he erroneously considered the shales of the Arroyo Hondo formation to be the equivalent of the Kreyenhagen shales to the south and the overlying "Domijean sands" were thought to represent a third, and upper, member of the Tejon in this area. The white shales above the "Domijean," the equivalent of the Kreyenhagen shales of the Reef Ridge section, were called the Monterey shales and considered to be of Miocene age. In a later paper entitled "A Further stratigraphic study in the Mount Diablo Range of California" Anderson (1908) noted that the shales below the "Domijean sands" were not the correlative of the Kreyenhagen shales to the south and considered them to be of probable Martinez age. The Domijean was still referred to the Tejon and considered as the equivalent of the Avenal sands to the south of Coalinga.

During this year the United States Geological Survey began the publication of a series of bulletins upon the geology of the San Joaquin Valley, including the area here studied. The first of these, by Ralph Arnold & R. V. Anderson, "Preliminary report on the Coalinga oil district, Fresno and Kings counties, California" (Bulletin no. 357),

was issued in 1908. The Avenal sands and the Kreyenhagen shale of F. M. Anderson were referred to as the lower sandstone and upper shale members of the Tejon formation. The following year (1909) a second paper by Arnold, "Paleontology of the Coalinga district, Fresno and Kings counties, California" (Bulletin no. 396), listed 52 species from the "Tejon (Eocene)" of Coalinga. New Eocene molluscan species described were:

Tellina joaquinensis	*Meretrix gabbi*
Spiroglyphus (?) *tejonensis*	*Tritonidea kreyenhageni*
Pleurotoma domenginei	*Pleurotoma fresnoensis*

Pleurotoma guibersoni

In 1910 a third report by Arnold & Anderson, "Geology and oil resources of the Coalinga district, California" (Bulletin no. 398), followed the preliminary report in referring the lower sandstones and upper shales to the Tejon. North of Coalinga it was recognized that the upper portion of the shales below the Tejon sandstones were of Eocene age and the lower portion, called the "purple shales," were Cretaceous. The fossil lists and illustrations of the 1909 report were reprinted.

A fourth report in the series, in 1911, entitled "Preliminary report on the geology and oil prospects of the Cantua-Panoche region, California" (Bulletin no. 431), by R. V. Anderson, referred the concretionary sands of the Cantua sandstone member of the Arroyo Hondo formation to the Cretaceous. The overlying shales were considered to be of Eocene age, and with the upper sandstone were referred to the Tejon.

During the following year (1912) an important paper by E. T. Dumble appeared in the Journal of Geology. In studying the Eocene rocks north of Oil City Camp in the Salt Creek-Cantua region two horizons were recognized, the upper being referred to the Tejon and the lower to the Martinez. His Martinez horizon, however, also included the lower portion of the shale series which Arnold & Anderson had referred to the Cretaceous. The most important contribution is the apparent appreciation of the significance of the conglomeratic horizon. In a portion of the area this occurs between the upper white sandstone member of the Arroyo Hondo formation and the Domengine formation (of this paper). Dumble noted that it marked the base of the upper formation rather than the place where occurs the sharp change in lithology between the clay shales and the white sandstones as most previous and subsequent writers have placed it.

The appearance in 1915 of Anderson & Pack's "Geology and oil resources of the west border of the San Joaquin valley north of Coalinga, California," a fifth report issued by the United States Geological Survey (Bulletin no. 603), was of great importance. In this study the Cantua sandstone and Clay shale members of the lower horizon were differentiated and were questionably referred to the Martinez formation. It was noted (66 and 67) that the faunas "contain many species that are present in the overlying Tejon, and on the whole probably resemble the fauna of the Tejon as known in other regions more closely than they do that contained in the Martinez at the type section near San Francisco Bay. Yet, as these beds contain such Lower Eocene fossils as *Turritella pachecoensis*, *Arca biloba*, and *Glycymeris veatchi* var. *major*, and rest unconformably below beds that contain a typical Tejon fauna they cannot well be mapped as Tejon and must either be designated by a new formation name or be correlated tentatively with the Martinez until more evidence regarding their true position is available." The Martinez species which they listed were apparently obtained from strata of Martinez age which have been recognized recently on the south side of Panoche Canyon, and were erroneously included by Anderson & Pack in their Martinez (?) formation. The authors recognized that the contact between the Cretaceous and the Eocene occurred between the shales of the Upper Cretaceous, which they designated as the Moreno shales, and the shales of their Martinez (?) formation. They were the first to indicate definitely that an unconformity occurred between the two horizons both to the north of Coalinga and in the Vallecitos area. The upper contact of their Tejon (Domengine) formation was recognized as a probable unconformity and the overlying Kreyenhagen shales were questionably referred to the Oligocene.

In 1916 Dickerson, in his "Stratigraphy and fauna of the Tejon Eocene of California," discussed (422–435) the "Tejon Group, Cantua District, Coalinga Quadrangle." The stratigraphical discussion is based entirely upon the earlier paper by Dumble (1912) and no mention is made of Anderson & Pack's more recent paper. The faunas were discussed in some detail and a list of 66 species, of which 57 were mollusca, 10 determined only to the genus, was given for locality 1817 in the lower zone. No Martinez species were found and the fauna was tentatively considered as representative of his *Turbinolia* zone as defined in the Mount Diablo area. A fauna of 87 molluscan species was listed from the "White Sandstone Member" and the

TABLE 1.
HISTORY OF THE EOCENE CORRELATIONS NORTH OF COALINGA, CALIFORNIA.

WHITE, 1885 BECKER, 1887	STANTON, 1896	F.M. ANDERSON, 1905	F M. ANDERSON, 1908	ARNOLD AND R. ANDERSON, 1910	DUMBLE, 1912	R. ANDERSON AND PACK, 1915	DICKERSON, 1916	CLARK, 1921	CLARK, 1927	VOKES THIS REPORT	AGE	
CHICO-TEJON SERIES		MONTEREY SHALES	KREYENHAGEN SHALES	TEJON FORMATION	OLIGOCENE (?) SHALES	KREYENHAGEN SHALES	OLIGOCENE SHALES	KREYENHAGEN SHALES	KREYENHAGEN SHALES	TUMEY SHALE		OLIG.
							WHITE SHALES: SIPHONALIA SUTTERENSIS ZONE ?			KREYENHAGEN FM.	TEJON	EOCENE
	TEJON GROUP	TEJON: DOMIJEAN SANDS	TEJON FORMATION		TEJON FORMATION	TEJON FORMATION	TEJON FORMATION: RIMELLA SIMPLEX ZONE	TEJON FORMATION	DOMENGINE FORMATION	DOMENGINE FORMATION	DOMENGINE STAGE	
								WHITE SANDSTONE MEMBER	WHITE SANDSTONE MEMBER	WHITE SANDSTONE MEMBER		
		KREYENHAGEN SHALES	MARTINEZ FORMATION		MARTINEZ FORMATION	MARTINEZ (?) FORMATION: CLAY SHALE MEMBER	TURBINOLIA ZONE	MEGANOS HORIZON: CLAY SHALE MEMBER	MEGANOS HORIZON: CLAY -SHALE MEMBER	ARROYO HONDO FORMATION: RAGGED VALLEY SHALE MEMBER	CAPAY STAGE	
						CANTUA SANDSTONE MEMBER		CANTUA SANDSTONE MEMBER	CANTUA SANDSTONE MEMBER	CANTUA SANDSTONE MEMBER		
				KNOXVILLE-CHICO GR.: PURPLE SHALE MEMBER		MORENO FORMATION		MORENO FORMATION	MORENO FORMATION	MORENO FORMATION		CRETACEOUS
	CHICO GROUP	CHICO GROUP	CHICO GROUP	CONCRETIONARY SANDSTONE MEMBER	CHICO GROUP	PANOCHE FORMATION	CHICO GROUP	PANOCHE FORMATION	PANOCHE FORMATION	PANOCHE FORMATION		

stratum was believed to be equivalent to the type Tejon. Both horizons were thus considered to be of Tejon age and the unconformity between the two was said to be "at most of secondary order, *i. e.* such as might separate two formations within a group." Twenty-one new species were described from these horizons.

In 1918 Clark announced the recognition of the Meganos group and subsequently (1921) discussed the distribution of this horizon in California. The Martinez (?) formation of Anderson & Pack was referred to the Meganos and the upper beds were considered to be of Tejon age.

In their paper on the fauna of the Type Tejon, F. M. Anderson & G. D. Hanna (1925) mention in the discussion of certain species, which where described from U. C. locality 672 and erroneously reported from the type Tejon, that the beds at locality 672 (upper horizon) "have not yet been proved to belong to the horizon of the Tejon at its type locality, and they may be older" (124, etc.). This was the first definite suggestion that the upper sandstones in the Coalinga Eocene section were not of Tejon age.

During the following year (1926) Clark published "The Domengine horizon, Middle Eocene of California," in which the upper sandstones of the section north of Coalinga were recognized as being older than the Tejon and were designated as the type section of the newly recognized horizon which was given the name "Domengine Formation." These beds were correlated with other strata throughout the California Eocene and the Domengine was shown to be a widespread and distinctive faunal unit.

In 1927 Stewart, in his study of "Gabb's California fossil type gastropods," recognized the Domengine formation as a faunal unit and certain of Gabb's types, including those described from the Vallecitos, are indicated as from this horizon, some being indicated as guide fossils in its recognition. Stewart's second paper on Gabb's fossil types, that on the pelecypods (1930), again recognized the significance of the Domengine horizon and distinguished Gabb's types which were from strata of that age.

In 1934, during the meeting of the Cordilleran Section of the Geological Society of America, Crook & Kirby described the Capay formation with the type locality in Capay Valley, west of Rumsey Hills on the western side of the Sacramento Valley. At the same time during the meeting of the Paleontological Society, Clark, Turner, Merriam, Berthiaume and the writer correlated several other localities

with the Capay formation and indicated that they were of a period of deposition younger than the Meganos and older than the Domengine. At this time I referred to the Capay stage the Eocene beds below the Domengine north of Coalinga which Clark had earlier (1921) correlated with the Meganos.

The evolution of the present concept as to the age relationships of the Eocene strata north of Coalinga is indicated in TABLE 1.

DOMENGINE STAGE: DOMENGINE FORMATION

Foreword

The Domengine formation was defined by B. L. Clark (1926: 104 and 105), with the type section on Domengine Ranch, north of Coalinga. The original description of this section was as follows:

> The Domengine formation in this section is not much over 100 feet in thickness. It is composed very largely of yellow-brown, medium-fine to coarse, fossiliferous sandstone. At the base of the formation is a thin bed of well rounded conglomerate characterized by the large number of black chert pebbles.
>
> The evidence for the unconformable relationship of the two formations* is as follows: (1) a well-defined irregular contact is found between the two series of deposits. This is general throughout the region; (2) boulders of the underlying white sandstone are found in the basal conglomerate of the Domengine; (3) there is a small difference in dip between the two formations and the underlying white sandstone of the Meganos thickens and thins very appreciably along the strike.

The name Domengine was first used (as Domijean) by F. M. Anderson (1905: 167) to designate a sandstone member in the Eocene north of Coalinga, the upper portion of which included the Domengine formation as here recognized, but the lower part included the white sandstones of the Arroyo Hondo formation.

The Domengine formation (restricted) occurs as an almost continuous line of outcrop throughout the entire area included in this report. The only interruptions of any extent occur between the north end of the Reef Ridge section near Zapato Creek and the southern portion of the Coal Mine section north of Alcalde Creek, and between the northern end of the Coal Mine section and the southern portion of the type section in the vicinity of Los Gatos Creek. In both areas the formation has been overlapped by the Etchegoin formation (Pliocene), and the evidence furnished by well cores indicates that the Eocene strata are continuous below the surface.

* The Domengine and the underlying "Meganos."

In order to obtain the most comprehensive knowledge of the Domengine faunal assemblage, it has been thought best to make intensive studies of the faunas of limited areas rather than to attempt a general survey of the entire section. For this purpose four regions* were selected in representative areas along the line of outcrop. These are here designated as (1) the "Type Section of the Domengine formation," including the region from Oil City north to Cantua Creek; (2) the "Vallecitos Section," including the Vallecitos Syncline, with special reference to the eastern end; (3) the "Coal Mines Section," between the overlaps north of Alcalde Creek and south of Los Gatos Creek; and (4) the "Reef Ridge Section," including the area from Garza Creek to a point approximately two miles south of Big Tar Canyon.

Type Section of the Domengine Formation

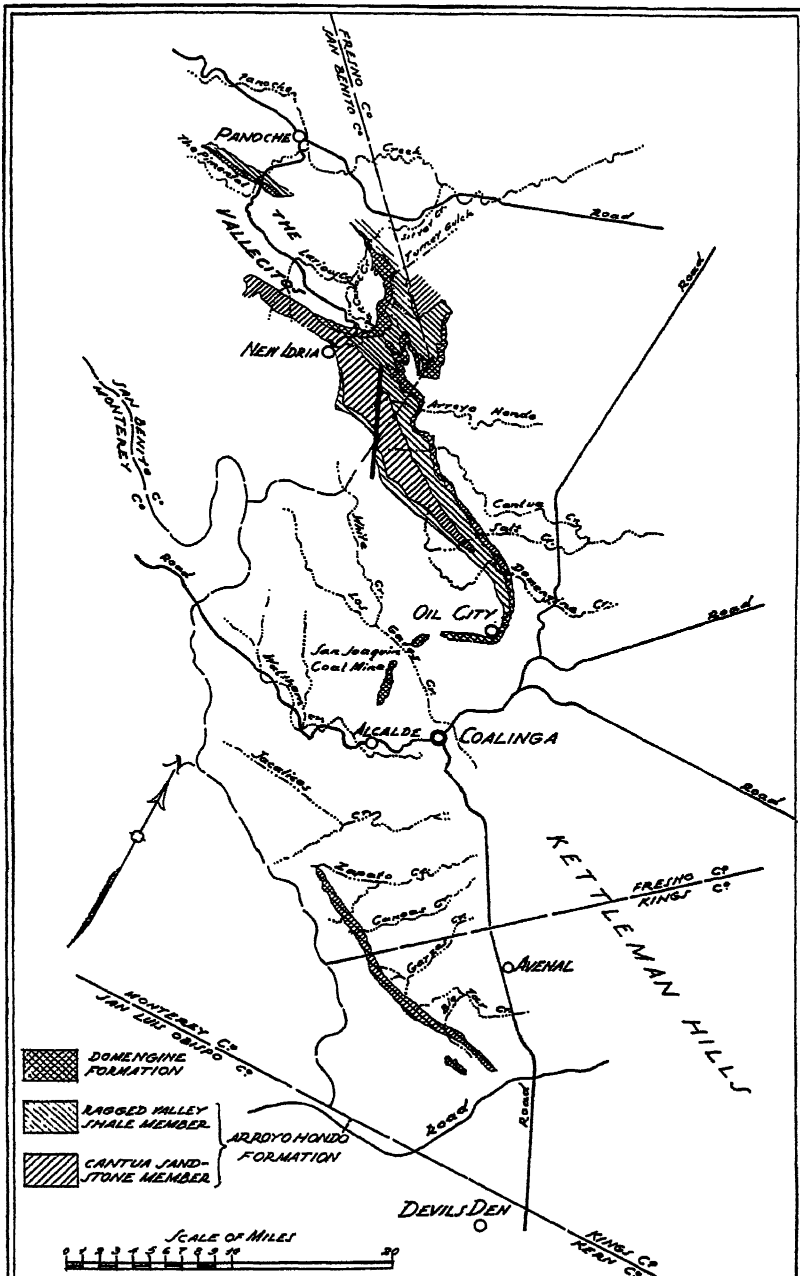
The area here included extends from Oil City Camp to Cantua Creek. The line of outcrop continues north along the entire length of the western border of the San Joaquin valley to the vicinity of Tesla, with only minor interruptions due to stream channels and local overlaps by later deposits.

In the region between Oil City Camp and Domengine Creek the formation is relatively thin and composed entirely of massive, yellow-brown to brown, sparingly fossiliferous sandstones, with a basal pebble conglomerate which contains a fauna of a large number of individuals of relatively few species. The characteristic fossils of this basal zone are:

Crassatella semidentata
Glycymeris sagittata
Macrocallista (Costacallista) domenginica
Nemocardium linteum
Pitar (Calpitaria) campi
Venericardia (Glyptoactis ?) domenginica

In the vicinity of Domengine Creek the sandstone is approximately 140 feet in thickness. Northward it becomes more abundantly fossiliferous and the thickness is irregular, due to local overlapping by the Kreyenhagen shale, which for a short distance immediately north of Salt Creek has almost entirely cut out this stratum. In this region the pebble layer is a less conspicuous feature; the pebbles are more sparingly present and of a smaller average size. The sandstones show

* See map on opposite page.


FRESNO CO
SAN BENITO CO
Panoche
PANOCHE
The Pimental
Creek
Road
THE VALLECITOS
Silver Cr.
Tumey Gulch
Larious Cr.
Road
NEW IDRIA
SAN BENITO CO
MONTEREY CO
Arroyo Hondo
Cantua Cr.
Salt Cr.
White Cr.
Road
Domengine Cr.
Road
Los Gatos Cr.
OIL CITY
San Joaquin Coal Mine
Waltham Cr.
ALCALDE
COALINGA
Jacalitos Cr.
Road
KETTLEMAN HILLS
Zapato Cr.
Canoas Cr.
FRESNO CO
KINGS CO
Garza Cr.
AVENAL
Big Tar Cr.
MONTEREY CO
SAN LUIS OBISPO CO
DOMENGINE FORMATION
RAGGED VALLEY SHALE MEMBER
CANTUA SANDSTONE MEMBER
ARROYO HONDO FORMATION
Road
Road
DEVILS DEN
SCALE OF MILES
0 1 2 3 4 5 6 7 8 9 10 20
KINGS CO
KERN CO

poor sorting, being predominantly of subangular quartz grains in a matrix of clay. Pebbles of gray to black cherts, generally well rounded, are scattered throughout but are never sufficiently abundant to permit the use of the term "conglomerate" at horizons above the basal portion of the formation.

In the vicinity of Oil City Camp a gray, sandy clay-shale a few feet in thickness lies above the sandstone. It contains a foraminiferal fauna which was said by Church (1931: 204) to be of Domengine age. According to Jenkins (1931: 144) these shales contain *Pecten interradiatus* Gabb, which throughout the rest of the region he considered to be diagnostic of the basal portion of the Kreyenhagen shales. They appear to be of local occurrence, possibly due to overlapping by the overlying Kreyenhagen (restricted).

The molluscan fauna of the type section of the Domengine Formation as at present known consists of 99 species: Pelecypoda 28, Scaphopoda 3, Gastropoda 47, and Cephalopoda 1.

Vallecitos Section

The Vallecitos section, as here defined, includes the strata involved in the Vallecitos syncline, extending eastward beyond the Vallecitos proper into Tumey Gulch, and westward beyond Griswold Canyon for an undetermined distance along the northern side of The Pimental. The southern flank on the syncline has been complexly faulted in The Pimental, and the Eocene is not exposed beyond the western end of the Vallecitos.

The Domengine formation in the eastern portion of the syncline may be separated on a lithologic and faunal basis into two members. The lower member consists of soft, gray, sandy shales and shaly sandstones containing an abundant but usually not well-preserved marine fauna. This member, which is slightly more than 100 feet in thickness, resembles the underlying sandy shales of the Ragged Valley Shale member of the Arroyo Hondo formation, but as both break down easily under weathering no actual contact has been definitely recognized.

The upper member, approximately 800 feet thick, is composed of white, red, and varicolored massive sandstones, with interstratified "chocolate-colored" shales containing abundant plumbojarosite and carbonaceous material. Near the center of the member is a stratum of coal, generally only a few inches in thickness; it is reported to have

reached a maximum thickness of 38 feet in a coal mine (now flooded) on the Ashurst Ranch, and is more than 4 feet thick near the head of De Los Reyes Canyon. The sandstones show a marked development of crossbedding and channeling and are generally of great thickness. The basal stratum of the upper member has a maximum thickness of 72 feet near San Carlos Creek.

In the western end of the Vallecitos the basal marine member has not been definitely recognized. Material in the State Survey Collection (locality A-1366 of this paper) contains marine species which suggest that, unless the collection has been mixed with material from other localities of similar age, the marine member must be present. The upper member is well developed and on the southeastern flank of Bucks Peak it can be seen resting, with a slight difference in dip, upon the Cantua member of the Capay horizon. A section measured along Griswold Canyon, in which the basal 100 feet are not exposed, indicates a thickness in the neighborhood of 460 feet, the upper 360 feet showing an alternation of white and brown sandstones and chocolate-brown shales similar to that noted near San Carlos Creek. The lower chocolate shale contains abundant, poorly preserved leaf-impressions.

This area was examined in reconnaissance fashion only, and complete fossil collections were not made. With the exception of locality A-1366, the fauna is of a distinctly brackish-water facies. The material here considered as from locality A-1366 is in the State Survey collections, labeled "10 miles west of Griswold's" by Gabb. All the information obtainable from old maps, residents of the region, and Whitney's description of the area (1865: 56) indicates that the road traveled was through Griswold Canyon, along the general line of the present road. The Eocene at the western end of the Vallecitos, here discussed, is the only stratum of this age to be encountered between San Juan and New Idria. It can not, however, have been more than 5 miles from Griswold's. The fauna of Gabb's locality is certainly of Domengine age, but contains elements which are more typically marine than any of the species collected by the writer. With these marine forms are associated, however, the majority of the species which are known to occur in this area. Two possibilities which might explain this seeming discrepancy are: (1) that Gabb obtained collections from a fossiliferous horizon not discovered during the present study; (2) that Gabb's collections were mixed with material from some other Domengine locality. In view of the second possibility, the several new species in the collection have not been recorded here.

Coal Mines Section

The Domengine formation in the vicinity of the San Joaquin and California Coal Mines northwest of Coalinga is approximately 150 feet in thickness, and is composed entirely of sandstones. The basal sands are soft, yellowish, and gypsiferous in character, but the major portion of the sediments are hard calcareous sandstones with abundant carbonaceous material. Interbedded are relatively thick coal seams which have been mined in former years. Near the top of the formation is a persistent stratum of coarse sandstone containing abundant fossils which are generally preserved only as molds, although peculiarly enough an echinoderm (*Cassidulus californicus* Anderson), a *Spiroglyphus*, and abundant crab-claws are usually well preserved. This is probably the bed that yielded the typical marine forms listed by Cooper in Watts (1894: 56, 57), and the poor preservation accounts for the number of misidentifications.

A shale zone, similar to that noted above the sandstone at Oil City Camp, overlies the sandstones in this area and was referred by Church (1931: 204) to the Domengine. Megafossils are absent, and the shale is brown, somewhat siliceous and platy with diatoms and abundant Radiolaria. The lithology is more suggestive of the Kreyenhagen shale. As the Domengine formation in this locality represents extremely shallow water deposition and as all available evidence suggests relatively deep water deposition for these shales, it has seemed best to exclude them from the Domengine formation at this time.

The fauna recognized in the Coal Mines section consists of 39 species, Pelecypoda 23 and Gastropoda 16, excluding the poorly preserved forms from the "Echinoderm-Spiroglyphus layer" which are only questionably identifiable as to genus.

Reef Ridge Section

As exposed along the western side of Reef Ridge, the Domengine formation has a maximum thickness of slightly less than 500 feet near Big Tar Canyon. The basal member is a conglomerate normally only a few feet in thickness; toward the northern limits of the exposed section it is more than 100 feet thick. The pebbles range up to two or three inches in diameter, but average less than one inch; they are composed predominantly of well-rounded gray and black cherts with

a minor amount of porphyritic fragments, generally of a basic type. Similar pebbles are abundant in the thick intraformational conglomerates in the immediately underlying Cretaceous deposits, and the Domengine material was evidently derived from either the same source or the Cretaceous conglomerates themselves.

The sandstones are poorly bedded or massive, varying from conglomeratic to fine-grained, but usually rather coarse-grained and poorly sorted. They are arkosic, with subangular quartz grains and comparatively fresh feldspars in approximately equal proportions. Reed (1924: 730), who has made careful studies of the heavy minerals, notes the almost entire removal of the ferromagnesian minerals and a consequent concentration of the more stable types—up to 72% zircon in one sample.

Between the sands of the Domengine and the strata of typical Kreyenhagen lithology is a zone of friable sandstone with interbedded clay shales containing foraminifera. These were called by Von Estorff (1930: 1327, 1328) a "Transition Zone" between the Domengine and the typical Kreyenhagen, but were tentatively included in the Kreyenhagen. Hanna (1925) correlated them with the sandy shale immediately overlying the Domengine at Oil City Camp and with the clay shales of the Capay horizon (of this paper). Jenkins (1931: 143) reports the occurrence of *Pecten interradiatus* in these strata as the only megafossil present.

Approximately one mile south of Big Tar Canyon there is a lens of soft, micaceous sandstone underlying the Domengine conglomerate. The material weathers so easily as to make it impossible to obtain satisfactory determinations of the attitude of the strata. No fossils have been found and the beds have been referred to the Cretaceous, although there is a possibility that they may represent the Capay stage or a Lower Eocene zone not recognized elsewhere in the Coalinga district.

In the vicinity of Big Tar Canyon, and to the south, five exceedingly fossiliferous horizons have been noted, with more sparingly fossiliferous strata between. Careful collecting and study of these zones fail to indicate evolutionary development within the fauna and it is considered to be a definite unit throughout. The number of species found in the collections is 108: Pelecypoda 47, Scaphopoda 2, and Gastropoda 59.

Stratigraphic Relationships of the Domengine Formation

Throughout the entire length of its outcrop the Domengine formation is overlain by the siliceous shales of the lithologic unit which has been called the Kreyenhagen formation. The contact has been considered by many writers* to be transitional, although Anderson & Pack (1915: 68, 69, 75) were of the opinion that it was unconformable. Their reasons may be summarized as follows:

(1) The Tejon (Domengine) is missing in several areas, notably on the north side of the Vallecitos, and the Kreyenhagen rests upon the Martinez (?) (Arroyo Hondo). This may be due to non-deposition of the Tejon in these areas or to pre-Kreyenhagen erosion.

(2) The thickness of the Tejon (Domengine) is variable, ranging from less than 50 feet to more than 750 feet in relatively short distances.

(3) The marked difference in lithology and faunas of the formations suggests a break in sedimentation.

Jenkins (1931: 143), in a comprehensive study of the Kreyenhagen, concluded that "the lower boundary of the Kreyenhagen shale proper does not appear to be a distinct unconformity, though in places (as north of Oil City Camp) there is an indication of a break in depositional continuity. The lower contact, however, may be regarded as a disconformity."

The writer's investigations have yielded no certain evidence as to the exact nature of the immediate contact. In several places there is marked evidence of overlap by the Kreyenhagen upon the Domengine sandstones. This is particularly well shown on the north side of the Vallecitos immediately east of Griswold Canyon. However, several unconformities have been recognized within the Kreyenhagen (as a lithologic unit), and the nature of the exposures has not permitted a definite determination of what horizon in the formation is responsible for the overlap. East of San Carlos Creek a white sandstone boulder approximately 2 feet in diameter from the upper member of the Domengine was found in place in the Kreyenhagen approximately 15 feet above the contact with the Domengine.

The lower contact may be stated with more assurance to be unconformable. In the Coal Mine and Reef Ridge sections the Domengine

* See particularly Arnold & Anderson (1910: 62) and Von Estorff (1930: 1327).

rests upon rocks of Cretaceous age, with the Lower Eocene strata absent. North of Oil City the formation rests upon the Arroyo Hondo deposits in an unconformable contact which has been discussed by several writers. Clark (1921: 143–145; 1926: 104, 105) has summarized the discussions of the nature of the contact in the type section. In the eastern end of the Vallecitos there is a constant, well-marked difference in dip and strike between the Domengine and Arroyo Hondo and the Domengine rests upon the Cantua sandstone member west of San Carlos Creek, apparently due to pre-Domengine erosion of the Ragged Valley shale member. The similar lithologic nature of the soft, easily weathered sediments has not permitted a certain view of the absolute contact, but all field evidence indicates an unconformity between the two horizons.

Fauna

The molluscan fauna of the Domengine formation in the Vallecitos and Coalinga areas consists of 182 species. This number represents an incomplete view of the fauna as a whole and a considerable number of species are yet to be reported. This is particularly true in the case of the Gastropoda, of which a number of forms too imperfectly preserved to permit adequate generic or specific determination occur in the collections. A few of these, because of some particularly interesting feature, are here referred to without a specific name.

TABLES 2 and 3 summarize the specific status of the fauna.

TABLE 2

TABULAR SUMMARY OF THE DOMENGINE MOLLUSCAN FAUNA

	Pelecypoda	Scaphopoda	Gastropoda	Cephalopoda	Tota
Species previously described	44	1	54	1	100
New species	28	2	27	0	57
Species compared to described forms	5	0	2	0	7
Species recognized but not named	11	1	6	0	18
Total number of species	88	4	89	1	182
Generic and subgeneric groups	51	3	75	1	130

TABLE 3

CHECK-LIST OF THE DOMENGINE MOLLUSCAN FAUNA

PELECYPODA	Domengine																
	Type section	Vallecitos	Reef Ridge	Coal Mine	U. Arroyo Hondo	L. Arroyo Hondo	Tejon formation	Cowlitz formation	"Domengine" Mt. Diablo	"Domengine" Martinez	Tyee formation	U. Llajas formation	La Jolla formation	Capay, Sacramento V.	Lower Llajas	Umpqua formation	Meganos formation
Nucula cooperi			×			×								×			
Acila (Truncacila) decisa *var.*	×		×			×	×			×			×	×	×	×	×
Nuculana (Saccella) gabbii	×	×	×				×	×	×	×	×	×	?			×	
Nuculana (Saccella) chaneyi		×	×														
Porterius woodfordi		×	×			×							×				
Glycymeris sagittata	×	×	×	×	×	×	×	×	×	×	×		×			×	
Glycymeris *cf.* rosecanyonensis	×								×				×				
Glycymeris perrini	×	×	×				?			×		×	×			×	
Glycymeris reefensis			×						×								
Trigonodesma hornii	×	×		×			×						×			×	
Barbatia (Obliquarca) morsei		×		×									×			×	
Pinna *n. sp.*	×																
Pteria pellucida	×	×	×				×			×			×				
Exputens alexi				×													
Pedalion joaquinensis				×													
Ostrea idriaensis	×	×		×				×					×	×		×	
Ostrea idriaensis *var.* fettkei		×		×				×					×				
Ostrea aviculiformis?	×		×														
Ostrea *n. sp.*				×													
Pecten (?) *n. sp.*		×															
Spondylus carlosensis	×						×										
Pododesmus (Monia) inornatus		×		×									×			×	
Mytilus dichotomus		×		×				?								×	
Mytilus (?) *n. sp.*				×													
Brachidontes *cf.* cowlitzensis	×	×	×			×	×	×	×	×	×		×		×	×	×
Cardiomya turneri	×	×								×							
Cardiomya silverensis		×															
Cardiomya domenginica		×															
Crassatella *cf.* meganosensis	×														×		×
Crassatella mulates	×												×				
Crassatella uvasana semidentata	×		×	×									×				
Corbicula carlosensis		×		×													
Venericardia (Glyptoactis ?) domenginica	×	×	×				?		×								
Megacardita (Venericor) hornii joaquinensis			×														
Megacardita (Venericor) hornii carlosensis		×															
Megacardita (Venericor) hornii *cf.* calafia		×									×	×	×				
Megacardita (Venericor) aragonia smileyi	×	×										×					
Megacardita (Venericor) vallecitosensis		×		×													
Lucina (Here) taffana	×	×	×						×				×				
Miltha (Eomiltha ?) packi	×	×	×						×			×	×			×	
Myrtea (Myrtucina) roseburgensis		×														×	
Taras unisulcatus	×	×	×		×	×			×	×							
Taras (?) politus	×	×	×	×	×					×			×				
Plagiocardium (Schedocardia) brewerii	×	×	×	×			×	×	×	×		×				×	
Trachycardium (Agnocardia) sorrentoense	×		×						×			×	×		×		
Nemocardium linteum	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
Mercimonia bunkeri	×	×	×	?					×		×		×			×	
Pachydesma packardi	×		×		×												
Pachydesma kelloggensis mclurensis			×														
Pachydesma sulcataria		×	×									?					
Macrocallista (Costacallista) conradiana		×	?				×									×	
Macrocallista (Costacallista) domenginica	×		×		?												
Nitidavenus tejonensis	?					×					×				×	×	
Pitar (Calpitaria) campi	×		×						×								
Pitar (Lamelliconcha) avenalensis			×														
Pitar (Lamelliconcha) joaquinensis	×	×	×						×								
Pitar (Lamelliconcha) hornii *n. subsp.*	×		×														
Pelecyora aequilateralis		×											×			×	

TABLE 3 (*Continued*)

	Domengine																
PELECYPODA	Type section	Vallecitos	Reef Ridge	Coal Mine	U. Arroyo Hondo	L. Arroyo Hondo	Tejon formation	Cowlitz formation	"Domengine" Mt. Diablo	"Domengine" Martinez	Tyee formation	U. Llajas formation	La Jolla formation	Capay, Sacramento V.	Lower Llajas	Umpqua formation	Meganos formation
Pelecyora gabbi				×												×	
Tivelina idriaensis		×		×													
Tivelina (?) delicatina		×															
Tellina soledadensis	×	×	×		×				×		?	×	×			×	
Tellina joaquinensis				×					?								?
Tellina *cf.* longa		×	×						×	×							×
Tellina domenginensis	×		×														
Tellina *sp.*	×																
Macoma sheridani		×		×													
Gari texta	×	×	×							×		×	×		×		
Gari columbiana		×	×					×									
Gari eoundulata		×	×		×												
Donax lata		×											?				
Solen parallelus	×		×		?		?			×							×
Solen (?) domenginicus				×													
Solena (Eosolen) coosensis	×		×						×		×	×	×		×	×	
Solena (Eosolen) subverticala	×		×		×	×									×		?
Solena (Eosolen) *sp.*	×																
Spisula merriami	×	×	×						×		?					?	
Corbula (Caryocorbula) dickersoni	×		×					×	×								
Corbula (Caryocorbula) parilis	×	×	×						×	×	×		×	×		×	
Corbula (Caryocorbula) tomulata	×												×				
Corbula (Varicorbula ?) cliffensis		×	×										×				
Corbula domenginica				×													
Cuneocorbula torreyensis		×											×			×	
Cuneocorbula griswoldensis		×															
Teredo *sp.*	×	×	×														
Teredo (Kuphus) *sp. aff.* polythalamia	×	×															
SCAPHOPODA																	
Dentalium (Dentalium ?) stramineum	×						×							×			×
Dentalium (Antalis) apicostatum	×																
Dentalium (Laevidentalium) calafium	×	×	×														
CEPHALOPODA																	
Aturia myrlae	×					×						×	×	×	×		
GASTROPODA																	
Kleinacteon moodyi	×	×	×	×													
Scaphander (Mirascapha) costatus	×	×	×		×	×			×	×	×	×	×			×	×
Cylichnina tantilla	×	×	×			×	×			?	×	×			×	×	
Cylichna (?) (Cylichnopsis) compara				×										×			
Akera maga			×														
Megistostoma gabbianum	×	×	×		×	×			×	×	×		×			×	
Terebra californica	×	×	×							×							
Fusiturricula (Crenaturricula) crenatospira domenginica		×	×									×					
Eopleurotoma (?) traski			×														
Pleurofusia fresnoensis	×	×	×						×			×		×			
"Pleurotoma" domenginei	×																
Microsurcula (?) ligna				×													
Trypanotoma stocki	×																
Gemmula *cf.* violeta	×												×				
Domenginella claytonensis	×	×	×		×				×	×		×	×				
Surculites mathewsonii	×		×						×	×		×				×	
Cryptoconus cooperi		×	×									×		×	×	×	?
Exilia ucalia			×														
Conus hornii umpquaensis	×	×	×			?						×	×		?	×	
Conus caleocius			×									×					
Bonellitia (?) megapex	×	×	×														
Olivella *cf.* mathewsonii	×		×				×	×					×				
Ancilla (Spirancilla) gabbi	×		×			×	×		×		×	×	×	×			

TABLE 3 (*Continued*)

GASTROPODA	Domengine																
	Type section	Vallecitos	Reef Ridge	Coal Mine	U. Arroyo Hondo	L. Arroyo Hondo	Tejon formation	Cowlitz formation	"Domengine" Mt. Diablo	"Domengine" Martinez	Tyee formation	U. Llajas formation	La Jolla formation	Capay, Sacramento V.	Lower Llajas formation	Umpqua formation	Meganos formation
Coralliophila dubia		×												×			
Marginella (Leptegouana ?) hulini		×	×														
Mitra simplicissima		×	×									×	×				
Mitromorpha (?) parsonsi	×																
Uromitra (?) cretacea			×						×	×							
Voluta (?) eomagna	×																
Lyria andersoni	×		×									×				×	
Fusinus ucalius			×									×					
Harpa (Eocithara) clarki			×														
Umpquaia flangella		×		×					?								
Pseudoliva lineata			×							×		×					
Cryptochorda californica		×	×		×					×		×		×	×	×	
Janiopsis (?) kreyenhageni				×													
Molopophorus cretaceus	×	×								×							
Molopophorus antiquatus		×	×							×						×	
Molopophorus aequicostatus	×																
Muricopsis (?) whitneyi *var.*		×		×													
Pseudoperissolax blakei praeblakei	×					×						×	×	×	×		
Cymatium (Lampusia) *n. sp.*	×											×	×				
Ranella domenginica	×		×						×			×					
Ranellina pilsbryi	×		×				×		×			×					
Galeodea tuberculiformis	×	×	×						×	×	×	×	×				
Ficopsis remondii crescentensis	×	×	×		×	×			×	×	×	×	×	×	×	×	
Eocypraea castacensis	×	×	×									×					
"Cypraea" fresnoensis	×																
Rimella (Macilentos) macilenta	×	×	×						×			×					
Terebellum californicum		×	×									×					
Potamides carbonicola		×		×									×			×	
Bittium (?) dumblei	×		×							×							
Loxotrema turrita		×		×									×	×		×	
Keilostoma californicum		×	×														
Turritella buwaldana	×	×	×	?			?		×				×				
Turritella uvasana *n. subsp.*	×	×	×	×					×	×							
Turritella andersoni lawsoni	×		×									×			×		
Spiroglyphus (?) tejonensis	×	×	×	×	×									×			
Architectonica (Stellaxis) cognata	×	×	×						×	×		×			×	×	
Architectonica *n. sp.*			×														
Tectarius ligniticus				×								×					
Crepidula (Spirocrypta) inornata	×																
Calyptraea diegoana	×	×	×	×	×	×	×	×			×	×	×	×	×	×	×
Xenophora *n. sp.*	×		×														
Natica domenginica	×																
Natica clementensis			×														
Polinices (Polinices) gesteri	×	×			×	×								×		×	×
Polinices (Euspira) nuciformis	×	×	×			×	×	×	×				×	×			×
Neverita globosa	×	×	×	×									×	×	×	×	×
Neverita globosa reefensis			×					×									
Sinum obliquum	×	×	×			×	×	×	×				×				
Ampullella schencki		×	×														
Crommium andersoni		×		×												×	
Cernina (Eocernina) hannibali	×	×	×		×				×		×	×	×		×	×	
Amaurellina caleocia	×		×		×				×			?					
Amaurellina garzaensis			×														
Amaurellina (?) multiangulata		×															
Pachycrommium (?) clarki	×	×	×				×		×	×	×	×	×		×	?	
Acrilla (Ferminoscala) tejonensis	×													?			
Odostomia griswoldensis		×															
Niso polita			×							×				×			
Homalopoma umpquaensis domenginensis	×																
Nerita (Amphinerita) eorex			×														
Nerita (Theliostyla) triangulata		×		×									×				
Velates perversus			×												×		
Velates californicus			×												×		
Acmaea *n. sp.*		×															

CAPAY STAGE: ARROYO HONDO FORMATION

Deposits of Capay age are exposed in the Vallecitos syncline and in the Coalinga region north of Oil City Camp. To the south they have not been certainly recognized, although certain non-fossiliferous strata, which have been mentioned as occurring below the Domengine formation along Reef Ridge south of Big Tar Canyon, may be of this age.

The strata north of Coalinga have been referred by various writers to the Martinez, Meganos, and Tejon stages (see historical review) but no formational name has been formally assigned them. The name Arroyo Hondo formation has been suggested by Mr. E. R. Atwill* and is here applied to these strata, the type section being considered to be the exposures of these strata along the Arroyo Hondo, north of Coalinga, California. Two well defined members are to be recognized throughout this formation as exposed in the area studied. These were mapped and discussed by Anderson & Pack (1915: 58–67) as the Cantua Sandstone member and the Clay Shale member of their Martinez (?). The term Ragged Valley Shale member is here proposed for this latter, the typical locality being on Domengine Creek in Ragged Valley, north of Coalinga. Between Oil City Camp and Cantua Creek an upper white sandstone forms a third member. This was mapped by Anderson & Pack as a part of the Tejon (Domengine), but since it lies unconformably below the Domengine formation, as was pointed out by Clark (1921), it is now considered as representing an upper member of the Arroyo Hondo formation. No well preserved fossils have been found in this member, which is composed predominantly of medium-grained, angular, quartzitic sandstones, white and generally cross-bedded. The thickness is variable, ranging from 100 to 300 feet, apparently due to pre-Domengine erosion.

Between Oil City Camp and Salt Creek the Ragged Valley shale member forms the major portion of the formation. This member is predominantly a compact, non-laminated, slightly sandy shale, for which Anderson & Pack suggest the term "siltstone." Intercalated are lenses and beds of fine-grained, mainly quartzitic sandstones. Selenite is abundant throughout in large crystals and platy masses. Approximately 75 feet above the base of the formation is a remarkably persistent zone of green "glauconitic" sandstone. This stratum has a maximum thickness of approximately 2 feet, averaging 15 inches. It has been noted immediately north of Oil City Camp; at Salt Creek, where it is abundantly fossiliferous; on Cantua Creek; at Arroyo

* Personal communication.

Hondo; and near San Carlos Creek on the road to New Idria; and appears to represent a continuous horizon between these localities, with an outcrop length of more than 24 miles.

The Cantua Sandstone member appears just south of Salt Creek. It is exceedingly lenticular in character, reaching a maximum thickness of approximately 4,500 feet between the head of Tumey Gulch and San Carlos Bolsa in Township 17 S., Range 12 E. The member consists of massively bedded arkosic sandstones composed of approximately equal proportions of subangular quartz and feldspar fragments. Each stratum averages between 15 and 20 feet in thickness, and beds more than 50 feet thick are not rare. Toward the top intercalated thicknesses of shale similar to that of the Ragged Valley shale member appear between the massive sandstones, and the two members seem to grade into each other.

The Cantua member is entirely within the Ragged Valley Shale, and a basal portion of the shale, approximately 100 feet thick, appears to underly the Cantua throughout. An upper portion, approximately 500 feet in thickness 2 miles east of San Carlos Creek, commonly overlies the Cantua, although it is not present west of San Carlos Creek, due apparently to pre-Domengine erosion or overlap. The lenticular nature of the Cantua member suggests that it is to be regarded as of deltaic origin, being composed of materials derived from a river which must have emptied somewhere to the southwest of the present San Carlos Bolsa.

Stratigraphic Relationships

The Arroyo Hondo formation lies unconformably below the Domengine formation and upon the Cretaceous Moreno shale. The nature of the contact between the Arroyo Hondo and the Domengine has been discussed in the consideration of the latter horizon. The unconformity between the Arroyo Hondo and the Moreno is expressed in the absence of deposits of Martinez and Meganos age. Northward the Martinez is represented on the south side of Panoche Canyon, but is absent in the area studied. The Moreno formation and the Ragged Valley member are lithologically similar and both are easily weathered, so that the actual contact is difficult to locate. The dip and strike of the two formations are approximately the same, and it is not surprising that the early workers, considering the Capay to be of Martinez age in this area, were inclined to believe that they represented continuous

deposition. Dr. P. W. Reinhart has reported (oral communication) that the immediate contact was observed for a short distance just north of Oil City Camp, where the upper surface of the Moreno was remarkably flat with no evidences of physiographic relief on the old surface.

Fauna

The fauna here reported from the Arroyo Hondo formation occurs only in the Ragged Valley Shale member. Anderson & Pack (1915: 60) have noted the occurrence of a poorly preserved *Aturia* in the Cantua sandstone, but no fossils were found in this member by the writer. Two distinct faunal zones have been noted in the Capay: (1) that of locality 1817 in the "glauconitic" sandstone near the base of the formation, here designated the lower zone of the Capay; and (2) a small fauna obtained within the uppermost 100 feet of the shale member near Domengine Creek, here designated the upper zone of the Capay.

The molluscan fauna of the lower zone consists of 66 species: Pelecypoda 29, Scaphopoda 2, Gastropoda 34, and Cephalopoda 1. Of these forms 6 have been determined as to genus only, while there are 5 Pelecypoda and more than 20 Gastropoda represented by material too poorly preserved to permit their consideration at this time. The fauna of the upper zone consists of 31 species: Pelecypoda 15 and Gastropoda 16; of which 27 have been determined as to species. Table 4 gives a complete list of the species found in the Arroyo Hondo formation and their known occurrence in other West Coast Eocene localities.

Table 4

Check-list of the Arroyo Hondo Molluscan Fauna

PELECYPODA	1817—Lower Zone	Upper Zone				Capay formation	Marysville-Oroville	Lower Llajas fmtn.	Domengine fmtn.	Tejon formation	Meganos formation	Santa Susana shale	Umpqua formation
		4178	A—820	A—821	A—978								
Nucula cooperi	×					×	×		×				
Acila (Truncacila) decisa	×					×	×	×	×	×	×		
Nuculana (Saccella) hondana	×					×							
Calorhadia (Litorhadia) fresnoensis	×					×		×					
Jupiteria (Ledina) duttonae	×												
Porterius woodfordi	×								×				

TABLE 4—(*Continued*)

PELECYPODA	1817—Lower Zone	Upper Zone 4178	A—820	A—821	A—978	Capay formation	Marysville-Oroville	Lower Llajas fmtn.	Domengine fmtn.	Tejon formation	Meganos formation	Santa Susana shale	Umpqua formation
Trigonodesma hornii elusa	×						×				×		
Glycymeris sagittata	×		×				×	×	×	×			×
Glycymeris fresnoensis	×						×						×
Glycymeris perrini instabilis	×						×	×					×
Ostrea *sp.*			×										
Propeamussium mideocenicum	×												
Vulsella (?) clarki	×					×							
Brachidontes *cf.* cowlitzensis	×				×				×	×	×		×
Periploma eodiscus		×											
Cardiomya *n. sp.*	×												
Megacardita *sp.*	×												
Lucina (?) bramkampi	×												
Taras unisulcatus	×	×			×				×				
Taras (?) politus				×	×		×		×				
Plagiocardium (Schedocardia) brewerii hartleyense	×										×	×	
Nemocardium linteum	×	×	×	×	×		×	×	×	×	×	×	×
Eomeretrix lillisi	×												
Nitidavenus conradi	×										×		
Nitidavenus tejonensis	×							×	?			×	
Macrocallista (Costacallista) domenginica					?				×				
Macrocallista (Costacallista) domenginica capayana	×												
Pitar (Lamelliconcha) *sp.*		×			×								
Pachydesma packardi			×						×				
Tellina soledadensis			×						×				
Gari hornii umpquaensis	×												×
Gari eoundulata			×						×				
Solena (Eosolen) subverticala	×				×				×		?		
Solen parallelus				×					×		×		
Spisula capayana	×						?						
Corbula (Caryocorbula) parilis	×						×	×	×				
Corbula (Varicorbula) capayana	×												
Corbula rosecanyonensis	×		×		×								
SCAPHOPODA													
Dentalium (Laevidentalium) lighti	×												
Cadulus (?) *n. sp.*	×												
CEPHALOPODA													
Aturia myrlae	×					×		×	×				
GASTROPODA													
Acteon *n. sp.*	×												
Tornatellaea effingeri	×												
Tornatellaea *n. sp.*	×												
Scaphander (Mirascapha) costatus	×		×						×	×	×	×	×
Cylichnina tantilla	×							×	×	×			×
Megistostoma gabbianum	×		×						×				×
Terebra *n. sp.*	×												
Fusiturricula (Crenaturricula) crenatospira	×					×	×	×					×
"Turricula" holwayi	×						×						
Pleurofusia fresnoensis *var*	×						×		×				
Eosurcula capayana	×												
Gemmula wattsi	×					×	×	×			?		
Domenginella claytonensis					×				×				
Exilia *cf.* perkinsiana	×					×	×						
Exilia taliaferroi					×								
Conus hornii umpquaensis	×							?					×
Ancilla (Spirancilla) gabbi	×					×	×	×	×				×
Falsifusus marysvillensis	×					×	×						
Cryptochorda californica			×				×	×	×				×
Pseudoperissolax blakei praeblakei	×						×	×	×				
Cumia harrisi	×												
Galeodea sutterensis	×					×	×	×					×
Galeodea susanae		×			×			×					×
Ficopsis remondii crescentensis	×			×	×	×	×	×	×				×

TABLE 4 (*Continued*)

GASTROPODA	1817—Lower Zone	Upper Zone 4178	Upper Zone A—820	Upper Zone A—821	Upper Zone A—987	Capay formation	Marysville-Oroville	Lower Llajas fmtn.	Domengine fmtn.	Tejon formation	Meganos formation	Santa Susana shale	Umpqua formation
Ficopsis meganosensis packardi	×											?	×
Rimella (Macilentos) macilenta			?						×				
Rimella (Macilentos) macilenta oregonensis	×												×
Turritella andersoni	×					×							×
Turritella buwaldana			×						×				
Turritella buwaldana crooki	×					×	×						×
Turritella uvasana *n. subsp.*		×	×						×				
Spiroglyphus (?) tejonensis		×		×	×				×				
Architectonica (Stellaxis) cognata	×							×					×
Calyptraea diegoana	×		×		×	×	×		×	×	×	×	×
Polinices (Polinices) gesteri	×		×			×	×		×		×		×
Polinices (Euspira) nuciformis	×					×	×	×	×	×	×	×	×
Sinum obliquum	×								×	×			
Amaurellina hendoni	×											?	×
Amaurellina caleocia			×						×				
Cernina (Eocernina) hannibali			×		×			×	×				×
Pyramidella *cf.* etheringtoni	×												
Melanella coalingana	×												
Homalopoma wattsi	×					×	×						×
Calliovarica eocensis	×												

RELATIONSHIPS OF THE FAUNAL HORIZONS IN THE VALLECITOS AND COALINGA AREAS

The relationships of the faunas in the Vallecitos and Coalinga areas to each other may be summarized as follows:

Number of species in Domengine fauna	182
Number of species in the Arroyo Hondo formation, upper zone	31
Number of species in the Arroyo Hondo formation, lower zone	66
Arroyo Hondo upper zone species in Domengine fauna	23
Arroyo Hondo lower zone species in Domengine fauna	22
Arroyo Hondo lower zone species in upper zone	11

Of the 31 species in the upper zone of the Arroyo Hondo, only 27 are fully determinable and all but 4 of these are also present in the Domengine fauna. These 4 are:

Corbula rosecanyonensis *Exilia taliaferroi*
Periploma eodiscus *Galeodea susanae*

Corbula rosecanyonensis is known from the shales of the La Jolla formation near San Diego. Its absence and that of *Periploma eodiscus* in the Coalinga area is possibly to be explained as due to ecologic

factors, since the upper zone of the Arroyo Hondo is a shale facies and the Domengine fauna is from sandstones. The genera *Exilia* and *Galeodea* are represented in all three recognized faunal horizons by distinct species which are absent in any of the other horizons. The close relationship between the fauna of the upper zone and the Domengine formation suggests that the time interval represented in the unconformity between the two was not of long duration. On the other hand, the possible removal of some 500 feet of clay shales in the Vallecitos area west of San Carlos Creek by pre-Domengine erosion prevents too much emphasis of this factor.

In contrast to the close relationship between the upper zone and the Domengine faunas, there is the marked difference between the fauna of the lower zone and that of the Domengine formation. Only one third of the species present in the lower zone are common to the two faunas. In part this may be explained by differing ecologic conditions. A major factor, however, is the time interval which separated the deposition of the two horizons. This is well indicated by the presence of a number of species in the fauna of the lower zone which appear to be ancestral to forms present in the Domengine fauna. Notable among these are:

Possible Capay Ancestor:	Domengine Descendant:
Trigonodesma hornii elusa	*Trigonodesma hornii*
Glycymeris perrini instabilis	*Glycymeris perrini*
Plagiocardium (*Schedocardia*) *brewerii hartleyense*	*Plagiocardium* (*Schedocardia*) *brewerii*
Macrocallista (*Costacallista*) *domenginica capayana*	*Macrocallista* (*Costacallista*) *domenginica*
Spisula capayana	*Spisula merriami*
Fusiturricula (*Crenaturricula*) *crenatospira*	*Fusiturricula* (*Crenaturricula*) *crenatospira domenginica*
Gemmula wattsi	*Gemmula* cf. *violeta*
Rimella (*Macilentos*) *macilenta oregonensis*	*Rimella* (*Macilentos*) *macilenta*
Turritella andersoni	*Turritella andersoni lawsoni*
*Homalopoma umpquaensis**	*Homalopoma umpquaensis domenginensis*

* This species is present in the Capay formation at the type locality, but is not represented in the fauna of the lower zone north of Coalinga.

CORRELATION OF THE VALLECITOS-COALINGA EOCENE WITH OTHER PACIFIC COAST MARINE EOCENE DEPOSITS

Foreword

The Eocene faunas of the Pacific Coast of North America are as yet too little known to permit definite correlations based upon statistical analyses of the various faunas. In general, it may be said that the various basins of Eocene deposition appear to have offered such varied ecologic set-ups as to permit the contemporaneous development of notably different specific groups. Certain species, subspecies and varieties which seem to have had a broad range in ecologic requirements and a short geologic time-span are used as index-fossils in the correlations here proposed. Notable among these are the species of the genus *Galeodea.* The occurrence of the species of this genus in the Coalinga Eocene may be summarized:

Domengine formation:	*Galeodea tuberculiformis*
Arroyo Hondo formation, upper zone:	*Galeodea susanae*
Arroyo Hondo formation, lower zone:	*Galeodea sutterensis*

Other Eocene horizons, not represented in the region studied, also appear to have characteristic species of this genus. *Galeodea trituberculata* Weaver is known only from the Tejon and Cowlitz formations; *Galeodea sutterensis* subsp. *meganosensis* n. subsp. and *Galeodea* n. sp. (see systematic discussion) are present in the Meganos formation and its correlative, the Santa Susana formation. None of the species thought to be diagnostic of any horizon is known to occur in association with one considered to be characteristic of any other horizon. It is possible that *G. susanae* and *G. tuberculiformis* may be found associated in strata in the Llajas formation which appear to be transitional between the upper zone of the Capay stage and the Domengine stage, as there appears to have been continuous deposition throughout Capay and Domengine time in this basin.

The species of the genus *Exilia* may upon further study prove to be significant in this consideration. In the Coalinga Eocene the following species are found:

Domengine formation:	*Exilia ucalia*
Arroyo Hondo formation, upper zone:	*Exilia taliaferroi*
Arroyo Hondo formation, lower zone:	*Exilia* cf. *perkinsiana*

Exilia ucalia is also known to occur in strata of Domengine age in the Potrero Hills, while *Exilia* cf. *perkinsiana* is present in the type locality of the Capay formation and in beds of the same age at Marysville Buttes. *Exilia taliaferroi* is as yet known only from the upper zone of the Capay stage north of Coalinga. Only one other species, *Exilia diaboli* (Gabb) is known from strata correlated with the Domengine formation, while several species occur in the Tejon formation, none of which are known in any older deposits.

Correlations of the Domengine Formation

Number of species in Domengine fauna	182
Species also found in "Domengine" at Martinez	33
Species also found at Mount Diablo	43
Species also found in Upper Llajas formation (restricted)	45
Species also found in Tyee formation	26
Species found only in above localities and in the Domengine	31

While the number of species in common between any of the above localities and the fauna of the Domengine formation does not appear to be large, the relationships between the horizons are indicated more certainly when it is understood that these faunas have not been monographed in detail. The number of species in common between the fauna of the Domengine at Coalinga and correlated strata at Mount Diablo and at Martinez, for example, represents more than 50% of the known fauna from these areas. The Tyee formation has yielded a fauna of 49 species (Turner 1938: 19), slightly more than 50% of which are also found in the Coalinga Domengine.

Galeodea tuberculiformis occurs at all these localities and is associated with a number of species which are at present known only from strata of Domengine age and are believed to be diagnostic of this horizon. Among these species are:

Megacardita (Venericor) hornii calafia
Pitar (Calpitaria) campi
Pitar (Lamelliconcha) joaquinensis
Terebra californica

Fusiturricula (Crenaturricula) crenatospira domenginica
Pleurofusia fresnoensis
Exilia ucalia
Domenginella claytonensis
Conus caleocius
Uromitra (?) *cretacea*
Pseudoliva lineata
Molopophorus cretaceus
Molopophorus antiquatus
Ranella domenginica
Bittium (?) *dumblei*

Correlations of the Arroyo Hondo Formation

LOWER ZONE.—Number of determinable species in fauna	60
Species also found in Capay formation (type locality)	22
Species also found in Capay at Marysville Buttes and Oroville	24
Species also found in Lower Llajas of Simi Valley	17
Species found in lower zone, type Capay, Marysville Buttes, Oroville, and Lower Llajas	36
Species confined to these localities	21

The large number of species which have been found only in the lower zone of the Capay stage at Coalinga, and in the type Capay formation at Capay Valley, together with strata at Marysville Buttes and Oroville, and the lower portion of the Llajas formation in the Simi Valley, indicates a correlation between these deposits. In all these localities *Galeodea sutterensis* is found, and *Exilia perkinsiana* has been reported from all except the Lower Llajas. Other species which are known only from this horizon in California include:

Homalopoma wattsi
Nuculana (Saccella) hondana
Calorhadia (Litorhadia) fresnoensis
Glycymeris fresnoensis
Vulsella (?) *clarki*
Fusiturricula (Crenaturricula) crenatospira
"*Turricula*" *holwayi*
Falsifusus marysvillensis
Turritella buwaldana crooki

Turritella merriami Dickerson was described from the strata of Capay age at Marysville Buttes and the typical form appears to be characteristic of this horizon in the Sacramento Valley. This species is not present in the Coalinga section, but appears to be replaced by *T. andersoni*. Both species occur in association at the type locality

of the Capay formation. The occurrence of *T. merriami* (*sensu stricto*) in Eocene strata in San Emigdio Canyon at the south end of the San Joaquin Valley, considered to be of Meganos age by Clark (1926: 107), suggests that these are also referable to the Capay stage, lower zone.

Upper Zone.—As had been mentioned, *Galeodea susanae* Schenck seems to be the most characteristic species of the fauna of the upper zone of the Arroyo Hondo formation. The occurrence of this species in the middle portion of the Llajas formation suggests that these strata are to be correlated with this zone. The upper portion of the Capay formation at the type locality has as yet failed to reveal a well-preserved molluscan fauna. Stratigraphic superposition indicates that it is the probable equivalent of the Upper Capay of the Coalinga section.

Turner (1938: 5, 6) in his discussion of the Umpqua formation of Oregon divided that formation into the Lower and Upper Umpqua. In considering the Umpqua as developed at Glide, Oregon, he states:

> The presence of *Galeodea susanae* Schenck in the upper Umpqua beds at Glide suggests that they are younger than the beds west of Roseburg and the beds along the Middle Fork of the Coquille containing *Galeodea sutterensis* Dickerson which have been termed lower Umpqua.

The stratigraphic relationships of the faunas bearing the species of *Galeodea* in the Coalinga section confirms Turner's conclusions and indicates that the Umpqua formation as developed west of Roseburg is to be correlated with the lower zone of the Capay stage at Coalinga, while the Glide fauna is the correlative of the upper zone.

Relationship of the Coalinga Eocene to the Lower Eocene Horizons

The fauna of the Arroyo Hondo formation shows little relationship to that of the Meganos formation. Twelve of the 59 species in the lower zone are also found in the Meganos fauna, and only three of these appear to be confined to these beds. Two of these, *Trigonodesma hornii elusa* (Clark & Woodford) and *Plagiocardium* (*Schedocardia*) *brewerii hartleyense* (Clark & Woodford), appear to be ancestral to long-ranging species in the higher Middle Eocene and Upper Eocene horizons. The third species, *Nitidavenus conradi* (Dickerson), may prove to be subspecifically distinct when better preserved material is

collected from the Meganos formation. The other species which are present in the Meganos and the Arroyo Hondo all have a long geologic range and are of no significance for purposes of geologic correlation.

Relationship of the Coalinga Eocene to the Upper Eocene Horizons

Number of species in the Domengine fauna	182
Species also found in the Tejon fauna	23
Species confined to the Domengine and the Tejon	1
Species also found in the Cowlitz fauna	15
Species confined to the Domengine and the Cowlitz	2
Species found in both the Tejon and the Cowlitz	29
Species confined to the Domengine and to the Tejon and the Cowlitz	2
Species also present in the La Jolla fauna	52

Recent studies leave little doubt that the Tejon and Cowlitz faunas are of contemporaneous deposition and that the observable faunal differences are to be correlated with ecologic and facies factors. The fauna of the Tejon-Cowlitz, therefore, seems to encompass all the types of facies variation which are encountered in the Vallecitos-Coalinga Domengine section. The Cowlitz fauna has not been monographed in detail as yet and the total number of species present is not known. Anderson & Hanna's (1925) list of 130 molluscan species from the Tejon, and an estimate of 250 species for the combined fauna from these horizons is conservative. Therefore, the fact that there are only 29 species in common between the Domengine fauna and the combined fauna of these two horizons, together with the fact that only 2 of these species, *Gari columbiana* Weaver & Palmer and *Spondylus carlosensis* Anderson, are as yet unknown from other localities, indicates the great length of time which must have intervened between the periods of deposition of the two horizons. Furthermore, there are a number of species in the Cowlitz and Tejon formations which appear to have been derived from species present in the Domengine fauna. Among these may be listed:

Probable Domengine Ancestor:	Tejon-Cowlitz Descendant:
Megacardita (Venericor) hornii joaquinensis	*Megacardita (Venericor) hornii clarki*
Pitar hornii n. subsp.	*Pitar hornii*
Tellina soledadensis	*Tellina tehachapi*
Gari hornii umpquaensis	*Gari hornii*
Conus hornii umpquaensis	*Conus hornii*

Ficopsis remondii crescentensis	*Ficopsis remondii*
Pseudoperissolax blakei praeblakei	*Pseudoperissolax blakei*
Neverita globosa	*Neverita secta*
Muricopsis whitneyi var.	*Muricopsis whitneyi*
Terebra californica	*Terebra* n. sp. (*T. californica* of Anderson & Hanna, 1925)
Crepidula (*Spirocrypta*) *inornata*	*Crepidula* (*Spirocrypta*) *pileum*

SYSTEMATIC PALEONTOLOGY

Foreword

SPECIES CONCEPT.—In the systematic discussions of the species which occur in the Vallecitos-Coalinga Eocene faunas the writer has attempted to base his conclusions as to the specific, subspecific, or varietal rank of the forms studied upon the following concepts:

1. A *species* is not a static element, but is composed of a group of forms which are intergradational and more closely related to each other than to any other group of forms.
2. A *subspecies* represents a group of individuals related to the specific mean but distinguishable by the presence or absence of some definable character, with intergradations between the subspecific and the typical form. The imperfections of the paleontologic record often make the discovery of these intergradations difficult or impossible and the matter of the specific or subspecific ranking to be accorded a group becomes dependent upon the probability of the presence or absence of intergradation.

In recent vertebrate faunas subspecific groups have been much studied. They appear to be present in well marked geographic areas, and to be a probable result of response to ecologic factors. In fossil faunas subspecies are also to be recognized in the stratigraphic sequence. The fossil subspecies, marking a stage in the evolution of the specific group, are believed to be of great significance in the determination of the finer stratigraphic zones.

3. A *variety* represents a group differing from the typical in definable characters in its maximum development, but intergrading with the normal type with which it is found in association.

The factor of association with the typical form has been made the major basis in the determination of subspecific or varietal status given a group in this report. The variety, occurring in association

with the normal type, is not as a rule significant in the determination of the stratigraphic sequence. Hence it has been deemed unwise to describe formally and to name the varietal groups recognized.

NOMENCLATURE OF TYPES.—The following nomenclature has been used in the designation of type specimens:

Holotype: The individual specimen designated to represent the species in formal description. In general, the holotype is considered to represent the average or characteristic form.

Paratype: A specimen, other than the holotype, used in the description of the species. The paratype may represent a type of variation which occurs in association with, and is gradational into, the average form.

Syntype: One of two or more specimens used in the description of the species when the preservation of the material at hand is not sufficiently satisfactory to justify the designation of a holotype. The term cotype, when properly used, is synonymous, but has been misused to a great extent by a number of early workers in California paleontology in a sense synonymous with the term paratype.

Topotype: A specimen determined from material which has been collected at the locality from which the species was originally described.

Hypotype: A specimen used to further illustrate a species which has been described from some other locality or geologic horizon.

Lectotype: A specimen subsequently selected from among several syntypes.

SYNONYMY.—No attempt has been made to give complete synonymy for the various species discussed. The synonymy given is intended to include:

(1) The reference to the place of original description of the species.
(2) The reference to the place of original description of the species held to be synonymous with the species discussed.
(3) References to the previously reported occurrence of these species in the Vallecitos-Coalinga faunas.

DESCRIPTION AND DISCUSSION OF SPECIES

Class PELECYPODA

Order PRIONODESMACEA

Family NUCULIDAE

Genus NUCULA Lamarck 1799

GENOTYPE (by monotypy): *Arca nucleus* Linné. Recent, coasts of Europe.

Nucula cooperi Dickerson

PLATE 1, FIGURES 1, 2

Nucula cooperi Dickerson (1913) 290. *pl. 14, f. 2a, b* (described, Marysville Buttes).—Dickerson (1916) 426, 427, 431, 446 (loc. 1817).

Hypotype 15559;* loc. 1817; length 10.3 mm., altitude 8.0 mm.
Hypotype 15560; loc. 1817; length 8.3 mm., altitude 6.2 mm.

This species was described from the Capay horizon at Marysville Buttes. Dickerson's original drawings of the type are not good and a comparison with the type material and the material from loc. 1817 shows that the posterior end (described as the anterior end) is straighter and more sharply angulate at the posterior ventral margin and the ventral margin is not as rounded as indicated.

The hinge of the left valve has 9 or 10 teeth in the posterior row and 16 or 17 in the anterior row, the rows being separated by a ligamental pit which is small, elongate-trigonal and directed anteriorly. The first tooth of the posterior row is large and trigonal in shape; the other teeth are straight. The inner margins of the valve are crenulate, and the muscle-scars moderately large and rather deeply set; the pallial line is entire.

Dickerson's record of this species from the type region of the Tejon formation is based upon *N. vitis* Anderson & Hanna (1925: 175. *pl. 2, f. 14; text-f. 8*).

Genus ACILA H. & A. Adams 1858

GENOTYPE (by subsequent designation, Stoliczka 1871): *Nucula divaricata* Hinds. Recent, China Sea.

Subgenus TRUNCACILA Schenck; Grant & Gale 1931

TYPE SPECIES (by original designation): *Nucula castrensis* Hinds. Recent, Pacific Coast of North America.

* All types and figured specimens used in this report, unless otherwise stated, are deposited in the invertebrate collections of the University of California Museum of Paleontology at Berkeley, California.

Acila (Truncacila) decisa (Conrad)

PLATE 1, FIGURES 3, 4

Nucula decisa Conrad (1858) 322. *pl. 3, f. 19* (described, "Miocene" San Diego).
Nucula truncata "Gabb"; Anderson in Dumble (1912) 32 (Salt Creek).
Acila gabbiana Dickerson (1915) 50 (*nomen nudum*).—Dickerson (1916) 426, 430, 444 (loc. 1817), 481. *pl. 36, f. 1* (described, loc. 1817).—Clark (1921) 158 ("Meganos," north of Coalinga).—Anderson & Hanna (1925) 176 (described "from loc. 1817 (U. C. Coll.) north of Coalinga").
Nucula (Acila) gabbiana (Dickerson) Clark & Woodford (1927) 85 (type from U. C. loc. 1817).
Nucula (Acila) stillwaterensis Weaver & Palmer (1922) *pl. 8, f. 8* (described, near Vader, Wash.).
Acila lajollaensis M. A. Hanna (1927) 270. *pl. 25, f. 1, 3, 5, 7, 8, 12, 15* (described, La Jolla formation).
Acila decisa (Conrad) Merriam & Turner (1937) 99 (Lillis Ranch).
Acila (Truncacila) decisa (Conrad) Schenck (1936) 53–56. *pl. 3, f. 1–9, 11–15; pl. 4, f. 1, 2; text-f. 7 (22–27)* (revision).

Hypotype 15557; loc. 1817; length 7.6 mm., altitude 6.1 mm.
Hypotype 15558; loc. 1817; length 7.1 mm., altitude 6.0 mm.

Acila gabbiana, described by Dickerson from loc. 1817, agrees in all details with the types of *Acila lajollaensis* Hanna. Conrad described *Nucula decisa* from the same region, referring the species to the Miocene. The strata from which Conrad's material was secured are now known to be of Eocene age.

Acila (Truncacila) decisa (Conrad) VARIETY

PLATE 1, FIGURES 7, 8

Figured specimen 15747; loc. A-1165; length 7.0 mm., altitude 5.7 mm.

Only four specimens referable to the genus *Acila* have been found in the collections from the Domengine formation. They all differ from the typical *Acila decisa* (Conrad) in being more inflated and in possessing a shallow groove bounding the edge of the lunule. Similar forms occur in beds of contemporaneous age in the Eocene of Oregon.

Family NUCULANIDAE

Genus NUCULANA Link 1807

GENOTYPE (by monotypy): *Nuculana rostrata* (Gmelin) = *Arca pernula* Müller. Recent, boreal, Atlantic and Pacific.

Subgenus SACCELLA Woodring 1925

TYPE SPECIES (by original designation): *Arca fragilis* Chemnitz = "*Lembulus*" *deltoideus* Risso. Recent, Mediterranean Sea.

Nuculana (Saccella) gabbii (Gabb)

Nuculana gabbii Conrad (1866) 3 (*nomen nudum*). Not *Nuculana* "*gabbi* Conrad;" White (1885) 29 (name used for New Jersey, *Leda protexta*).

Leda gabbii "Conrad;" Gabb (1869) 197 (Griswold's).—Anderson (1908) 15 (Oil City).—Arnold (1909) 13, 16 (S. W. of Domengine's Ranch); (not *pl. 2, f. 8* = ? *N. washingtonensis* [Weaver]).—Arnold & Anderson (1910) 70, 72 (S. W. of Domengine's Ranch); (not *pl. 24, f. 8* = ? *N. washingtonensis* [Weaver]).—Dickerson (1915) *pl. 1, f. 1* (loc. 672).—Dickerson (1916) 431, 445 (in part). *pl. 36, f. 3* (between Domengine and Cantua creeks).
Leda vaderensis Dickerson (1915) 49, 52. *pl. 1, f. 3* (described, Cowlitz formation, Washington).
Leda cowlitzensis Weaver & Palmer (1922) 6. *pl. 10, f. 4* (described, Cowlitz formation, Washington).
Leda vogdesi Anderson & Hanna (1925) 177. *pl. 2, f. 8, 9* (described, Tejon). Not *Leda vogdesi* "Anderson & Hanna"; M. A. Hanna (1927) 259, 271 (La Jolla formation).
Leda gabbii "Gabb"; Anderson & Hanna (1925) 179 (Coalinga record).
Saccella gabbii "Gabb"; Stewart (1930) 55, 56 (synonymy), 57 (Coalinga record).

As shown by Hanna (1924: 170), *Nuculana Gabbii* Conrad (1866) is an absolute *nomen nudum*, without locality or description, and the species must be dated from Gabb's use in 1869.

Nuculana (Saccella) hondana NEW SPECIES

PLATE 1, FIGURES 9. 10

Leda "*gabbi* (Conrad)" Anderson (1908) 13 (Salt Creek).—Anderson in Dumble (1912) 32 (Salt Creek).—Dickerson (1916) 426, 427, 431 (in part), 445 (in part, loc. 1817); (not *pl. 36, f. 3*).—Clark (1921) 158 ("Meganos" N. of Coalinga).

Holotype 15561; loc. 1817; length 8.9 mm., altitude 4.8 mm.
Paratype 15562; loc. 1817; length 9.7 mm., altitude 5.1 mm.

DESCRIPTION.—Shell small, elongate, subtrigonal, moderately inflated; umbo nearly central; anterior and ventral margins broadly and regularly rounded; posterior margin rounded to the bluntly angulate rostrum; anterior dorsal margin varying from slightly concave to straight; posterior ventral margin slightly concave, the shell appearing distinctly equilateral; sculpture consisting of narrow, widely and regularly spaced concentric lines; a shallow, smooth groove extending from the beaks to the posterior point of the rostral margin; lunule and escutcheon long, narrow and well defined, the escutcheon crossed by a diagonal ridge.

COMPARISON.—*Nuculana hondana* may be distinguished from *N. gabbii*, with which it has heretofore been confused, by the bluntly rostrate posterior margin, the more equilateral outline, the straight rather than convex anterior dorsal margin, and the sculpturing of impressed lines rather than concentric ribbing; from *N. parkei* (Anderson & Hanna*) by differences in shape and sculpturing, and in the absence of "small, sharp ridges on the impressed area."

A specimen from the La Jolla formation, in the collections of the University of California, identified by Hanna as "*Leda vogdesi* An-

* Anderson & Hanna (1925) 179. *pl. 2, f. 10, 11;* as *Leda parkei*.

derson & Hanna," shows differences from *N. hondana* that are not more than subspecific, and appears to be genetically derived from the Arroyo Hondo species. It is not *Leda vodgesi* Anderson & Hanna* (=*Nuculana gabbii* (Gabb)).

Nuculana (Saccella) chaneyi NEW SPECIES

PLATE 1, FIGURES 11, 12

Syntype 15745; loc. A-1165; length 5.1 mm., altitude 3.1 mm.
Syntype 15746; loc. A-976; length 6.3 mm., altitude 3.3 mm.

DESCRIPTION.—Shell small, elongate; beaks low, opisthogyrate, slightly anterior; anterior dorsal margin slightly convex, sloping to the sharply rounded anterior end; ventral and posterior margins broadly rounded to the acute posterior end; posterior dorsal margin concave; escutcheon broad, incised, marked by a diagonal ridge from the beak nearly to the posterior end; lunule incised, narrower, and less well marked than the escutcheon; surface sculptured by broad, low, rounded ribbing separated by narrow incised interspaces; posterior area depressed, bounded by a well marked umbonal line to the posterior ventral margin, smooth except for coarse lines of growth.

COMPARISON.—*N. chaneyi* somewhat resembles *N. hondana* in outline but differs in the depressed posterior area; it differs from *N. parkei* (Anderson & Hanna) and *N. parkei coosensis* Turner† in lacking posterior umbonal ridges; from *N. gabbii* it may be separated by shape and sculpturing.

Named in honor of Dr. R. W. Chaney of the Department of Paleontology, University of California.

Genus CALORHADIA Stewart 1930

GENOTYPE (by original designation): *Leda pharcida* Dall. Bashi formation, Wilcox, Eocene.

Subgenus LITORHADIA Stewart 1930

TYPE SPECIES (by original designation): *Leda acala* Dall = *Yoldia aldrichiana* Harris. Bashi formation, Wilcox, Eocene.

Calorhadia (Litorhadia) fresnoensis (Dickerson)

PLATE 1, FIGURE 5

Leda fresnoensis Dickerson (1916) 426, 427, 431, 445, 483. *pl. 36, f. 2a, 2b* (described, loc. 1817).—Clark (1921) 158 ("Meganos," north of Coalinga).
Nuculana fresnoensis (Dickerson) Merriam & Turner (1937) 94, 96, 99 (Lillis Ranch).

Topotype 15563; loc. 1817; length 19.0 mm., altitude 10.4 mm.

* Anderson & Hanna (1925) 177. *pl. 2, f. 8, 9.*
† Turner (1938) 42. *pl. 5, f. 5.*

The hinge of this species is that of typical *Calorhadia;* the anterior tooth-row is the shorter, containing 18+ chevron-shaped, narrow teeth, smaller near the umbo; the posterior row has 24 chevron-shaped teeth which are smaller near the beak but more robust than the teeth of the anterior row. The ligamental pit is trigonal in shape, moderately wide and symmetrically placed between the two rows of teeth. The impressed lunule is wide and long, extending to the anterior dorsal extremity; the escutcheon is wide and long and extends to the posterior dorsal extremity, being divided by a diagonal ridge from beneath the umbos to the posterior dorsal edge near the posterior end.

In his check-lists Dickerson lists this species as occurring in the vicinity of Mount Diablo (1916: 445), but on page 427 gives it as one of the forms from loc. 1817 "which have not been reported from the Tejon at other localities or from the Martinez Group." No material substantiating the Mount Diablo record has been found.

Genus JUPITERIA Bellardi 1875

GENOTYPE (by subsequent designation, Dall 1898): *Nucula concava* Bronn. Pliocene, Italy.

Subgenus LEDINA Dall 1898

TYPE SPECIES (by original designation): "*Leda*" *smirna* Dall (new name for *Leda eborea* Conrad 1860, not 1856). Midway, Eocene, Alabama.

Jupiteria (Ledina) duttonae NEW SPECIES

PLATE 1, FIGURE 6

Holotype 15564; loc. 1817; length 5.5 mm., altitude 3.2 mm.

DESCRIPTION.—Shell small, elongate, subtrigonal, moderately inflated; umbos central, high, prominent; anterior, posterior, and ventral margins broadly and regularly rounded; slightly rostrate posteriorly with the rostrum barely ridged; lunule and escutcheon prominent, long, narrow, high, smooth, set off from the rest of the shell by a shallow groove; surface sculptured by fine, regularly spaced, concentric striae, nine to the one mm. interval on the center of the valve; hinge consisting of a slightly convex anterior and a slightly concave posterior series of chevron-shaped teeth.

COMPARISON.—This unique little species is not to be confused with any previously described from the Western Eocene. The high, centrally located umbos and the broad, rounded shape are distinctive. The genus has not previously been reported from the West Coast.

Named in honor of the writer's wife, Gertrude Dutton Vokes, whose assistance and encouragement have been of great value in the preparation of this report.

Family PARALLELODONTIDAE

Genus PORTERIUS B. L. Clark 1924

GENOTYPE (by original designation)· *Barbatia andersoni* Van Winkle = *Barbatia gabbi* Dickerson. Oligocene, Washington.

Porterius was originally described as a subgenus of *Parallelodon* Meek & Worthen 1866. It is present in the Middle Eocene and the Oligocene on the West Coast. The type species is from the Oligocene of Washington.

Porterius woodfordi (M. A. Hanna)

PLATE 1, FIGURE 13

Barbatia morsei "Gabb"; Anderson in Dumble (1912) 32 (Salt Creek).
Barbatia woodfordi M. A. Hanna (1927) 273. *pl. 27, f. 1, 6, 8, 10* (described, La Jolla formation).
Porterius woodfordi (M. A. Hanna) Reinhart (1937) 176, 177 (redescription, specimen from loc. 1817).

Hypotype 32472; loc. 1817; length (incomplete) 12.0 mm., altitude (incomplete) 7.2 mm.

The type is an immature specimen showing well-developed teeth across the entire area. Hypotype 32472, an adult, shows four chevron-shaped teeth anteriorly and two long transverse teeth posteriorly. The ligamental area is narrower and confined to the area posterior to the umbo. This species is rare in all horizons in the Coalinga area, four specimens found in the Arroyo Hondo formation (loc. 1817) and two worn individuals being questionably referred to this species from the Domengine formation (locs. A-819 and A-1014).

Family GLYCYMERIDAE

Genus GLYCYMERIS da Costa 1778

GENOTYPE (by tautonomy): *Glycymeris orbicularis* da Costa = *Arca glycymeris* Linné. Recent, Atlantic Coast of Europe.

Glycymeris sagittata (Gabb)

PLATE 1, FIGURES 18, 19, 20

Axinaea (Limopsis ?) sagittata Gabb (1864) 197, 235. *pl. 31, f. 267, a* (described, Tejon).
Axinaea sagittata Gabb (1869) 196, 249 (Griswold's).—Cooper in Watts (1894), 62 (Coalinga).
Axinaea veatchi Gabb; Cooper in Watts (1894) 57 (San Joaquin Coal Mine).
Pectunculus sagittatus Gabb; Stanton (1896) 1026 (New Idria).—Anderson (1908) 15 (Domengine's Ranch).—Watts in Anderson (1908) 15 (south of Oil City).
Glycimeris "sagittatus" (Gabb) Dickerson (1916) 430, 445. *pl. 36, f. 5a, 5b* (between Domengine and Cantua creeks).—(?) Dickerson (1916) 426 (loc. 1817).—Clark (1926) 114 (Coalinga).

Glycimeris sagittata Stewart (1930) 71, 72 (synonymy).—Turner (1938) 43. *pl. 6, f. 1, 2, 3* (Domengine).
Glycimeris hannibali Dickerson (1916) 430, 445, 483. *pl. 36, f. 8a, 8b* (described, Coalinga).—Clark (1926) 114 (Coalinga).—Stewart (1930) 72 (probably a synonym of *G. sagittata*).
? *Glycimeris kelsoensis* Weaver & Palmer (1922) 11. *pl. 8, f. 2* (described, Coal Creek, Washington).

Hypotype 15567; loc. A-1219; length 40.4 mm., altitude 41.5 mm.
Hypotype 15565; loc. 2293; length 33.0 mm., altitude 31.0 mm.
Hypotype 15564; loc. A-819; length 33.0 mm., altitude 32.4 mm.

This species is abundantly represented in the pebbly conglomerate at the base of the formation northward from Oil City and in the marine horizon of the Vallecitos. The forms in the conglomerate are in general larger in size than those from the type Tejon and are excellently preserved. The shell is smooth, radial ribbing on the surface being absent; upon weathering, the interspaces first appear as minute pitting, which rapidly deepens so that the radial ribs become prominent surface-features. The outline of the valves is variable; the most characteristic variations are figured.

There seems to be a slight progressive loss of ribs during the evolution of this species. A count of several specimens from various Eocene horizons in California shows:

Horizon	Average Number of Ribs	Minimum No.	Maximum No.
Tejon	44	39	48
Domengine	48	43	52
Capay	49	46	52

The Domengine specimens might be considered to represent a distinct subspecies or variety but, due to the fact that the amplitude of variation of the Tejon forms is such as to include the average number of ribs found in the Domengine forms, the writer hesitates to take that step until his observations have been confirmed by material from areas other than that with which he is here concerned.

The type of *G. hannibali* Dickerson bears a posterior depression or flexure from the beak to the straight posterior margin. This character is rarely found on any of the Tejon specimens and only occasionally occurs in those from the Domengine horizon. It is strongly developed on the forms from the Meganos, which were described as *Glycymeris major meganosensis* Clark & Woodford, but which appear to be more nearly related to *G. sagittata*, having the ribbing absent from the surface on unworn specimens.

Glycymeris cf. rosecanyonensis M. A. Hanna

PLATE 1, FIGURE 15

Cf. *Glycymeris rosecanyonensis* M. A. Hanna (1927) 273. *pl. 27, f. 4, 5, 9, 11* (described, La Jolla formation).

Hypotype 32579; loc. 672; length 4.7 mm., altitude 4.6 mm.

Glycymeris perrini Dickerson

PLATE 1, FIGURE 23

Glycimeris perrini Dickerson (1916) 430, 445, 482. *pl. 36, f. 6a, 6b, 6c* (described, between Domengine and Cantua creeks).—Clark (1926), 114 (Coalinga). Not *Glycymeris perrini* "Dickerson"; Stewart (1930) 73, 74. *pl. 7, f. 5* (= *G. perrini instabilis*).

Hypotype 31439; loc. A-1165; length 18.2 mm., altitude 17.3 mm.

This species is characterized by the presence of "double ribs" which appear as ribs only after weathering; on unweathered specimens the ribbing appears as a difference in shell-texture on an almost smooth surface.

Glycymeris perrini Dickerson instabilis Anderson & Hanna

PLATE 1, FIGURES 14, 16

Axinaea cor Gabb (1864) 198, 235. *pl. 31, f. 268, a* (described).
Glycimeris cor (Gabb) Dickerson (1916) 426, 427, 431 (loc. 1817). Not *Pectunculus cor* Lamarck (1805), 217; nor *Pectunculus* (*Axinaea*) *cor* Cossmann & Peyrot (1912) 251. *pl. 6, f. 13–6.*
Axinea gabbi Cossmann (1913) 64 (new name). Not *Glycymeris gabbi* Dall (1909) 108. *pl. 11, f. 5* (Coos Bay).
Glycymeris instabilis Anderson & Hanna (1925) 185 (new name).
Glycymeris tecolotensis M. A. Hanna (1927) 274. *pl. 27, f. 2, 3, 7* (La Jolla formation).
Glycymeris perrini Dickerson; Stewart (1930) 73 (in part). *pl. 7, f. 5.* Not *G. perrini* Dickerson.

Hypotype 15569; loc. 1817; length 7.1 mm., altitude 6.4 mm.
Hypotype 15570; loc. 1817; length 8.2 mm., altitude 7.1 mm.

Measurements of a large series of specimens show that *G. perrini instabilis* is slightly longer than high; typical *G. perrini* is slightly higher then long. Also, the straight sloping posterior margin is shorter on the subspecies than on typical *G. perrini.* The beaks are more centrally placed, giving the subspecies *instabilis* a more equilateral appearance.

Glycymeris perrini instabilis occurs in the Coalinga region only in the Arroyo Hondo formation and does not occur in the collections from the Domengine; *Glycymeris perrini* is found only in the Domengine collections.

Glycymeris reefensis NEW SPECIES

PLATE 1, FIGURE 21

Holotype 15571; loc. A-1165; length 11.3 mm., altitude 10.8 mm.

DESCRIPTION.—Shell small, inflated; umbos central, prominent; cardinal area straight, slightly more than half the length of the shell; anterior, posterior, and ventral margins regularly and evenly rounded; posterior area not defined; surface smooth except for minute arrow-shaped pittings similar to those found in *G. sagittata;* interior of shell not seen.

COMPARISON.—*Glycymeris reefensis* may be distinguished from *G. sagittata* by its round outline and shorter cardinal area; from all other described West Coast Eocene species it may be distinguished by its smooth shell with arrow-like pittings.

Glycymeris fresnoensis Dickerson

PLATE 1, FIGURE 17

Glycimeris fresnoensis Dickerson (1916) 426, 427, 431, 483. *pl. 36, f. 7* (described, loc. 1817).—Clark (1921) 158 ("Meganos" N. of Coalinga).

Topotype 15593; loc. 1817; length 13.5 mm., altitude 13.0 mm.

The type is an immature specimen in which the ribbing is sharper than is characteristic on adult individuals. The statement that the "beak is decidedly twisted" is not borne out by a study of the type material, nor is it indicated in the figure accompanying the original description.

Glycymeris fresnoensis appears to be a characteristic species of the Capay stage, occurring both at Capay and in the same horizon in the Oregon Eocene. Dickerson's record of the species in the "Type Tejon" was based upon *G. verticordia* Anderson & Hanna (1925: 183. *pl. 2, f. 5; pl. 11, f. 1*). The species does not occur in the Domengine collections. In his list of Tejon species reported in California (1916: 445), Dickerson has placed his check-mark in the wrong column, recording this species from the "Concord Quadrangle, North of Mount Diablo, South of Mount Diablo" and not from the "Coalinga District."

Family ARCIDAE

Genus TRIGONODESMA Wood 1864

GENOTYPE (by subsequent designation, Winckworth 1934): *Arca lissa* Bayan. Eocene, England.

Reinhart, who has recently studied the California *Arcidae*, questionably places *Halonanus* Stewart 1930, type (by original designation) *Noetia pulchra* Gabb, in the synonymy of *Trigonodesma*.*

* Reinhart (1935) 51–53.

Trigonodesma hornii (Gabb)

PLATE 1, FIGURES 24, 27

Arca hornii Gabb (1864) 194, 235. *pl. 30, f. 263* (described, Tejon).—Dickerson (1915) *pl. 1, f. 4* (loc. 672).—Dickerson (1916) 430 (in part), 444 (in part). *pl. 36, f. 4* (loc. 672).—Clark (1926) 114 (Coalinga).
Halonanus hornii (Gabb) Stewart (1930) 79 (synonymy), 80 (Parson's Peak, Coalinga). *pl. 10, f. 6.*
Trigonodesma hornii (Gabb) Reinhart (1935) 53.

Hypotype 32544; loc. 672; length 10.5 mm., altitude 7.4 mm.

Trigonodesma hornii (Gabb) elusa (Clark & Woodford)

PLATE 1, FIGURE 22

Arca "*horni* Gabb," Anderson in Dumble (1912) 32 (Salt Creek).—Dickerson (1916) 426, 430 (in part), 444 (in part) (loc. 1817).
Arca hornii elusa Clark & Woodford (1927) 87. *pl. 14, f. 6* (described, Meganos formation).
Trigonodesma hornii elusa (Clark & Woodford) Reinhart (1935) 53.

Hypotype 15594; loc. 1817; length 4.3 mm., altitude 3.1 mm.

This subspecies occurs only in the collections from locality 1817 (Capay stage), where it is not common. Described from the Meganos formation, it is probably ancestral to *T. hornii* from the Domengine and Tejon formations, from which it differs in its less well developed cardinal area and the shorter hinge-line, which is not so long posterior to the beaks.

Genus BARBATIA Gray 1842

GENOTYPE (by subsequent designation, Gray 1847): *Arca barbata* Linnaeus. Recent, Mediterranean Sea.

Subgenus OBLIQUARCA Sacco 1898

TYPE SPECIES (by original designation): *Arca modioliformis* Deshayes. Eocene, Paris Basin, France.

Barbatia (Obliquarca) morsei Gabb

PLATE 1, FIGURES 25, 26, 28, 29

Barbatia morsei Gabb (1864) 216. *pl. 32, f. 286* (described, San Diego).—Arnold (1909) 13, 16. *pl. 3, f. 8* (San Joaquin and California Coal Mines).—Arnold & Anderson (1910) 70, 73. *pl. 25, f 8* (San Joaquin and California Coal Mines).—Stewart (1930) 87 (synonymy). *pl. 8, f. 7.*
Arca (*Barbatia*) *morsei* Gabb; Anderson (1905) 166 (coal mines).
Barbatia (*Obliquarca*) *morsei* (Gabb) Reinhart (1935) 25.

Hypotype 32537; loc. 7155; length 15.5 mm., altitude 9.4 mm
Hypotype 15573; loc. 7155; length 15.0 mm., altitude 7.7 mm.
Hypotype 15574; loc. 7155; length 19.0 mm., altitude 10.2 mm.
Hypotype 15575; loc. A-972; length 19.8 mm., altitude 10.8 mm.

This species is common in the carbonaceous strata in the vicinity of the San Joaquin and California Coal Mines northwest of Coalinga; it has not been found in deposits of an apparently similar ecologic nature in the Vallecitos. The species was described from the San

Diego Eocene, and also occurs in the Oregon Eocene deposits. It has not been found in either the Meganos or Tejon formations.

Family PINNIDAE

Genus PINNA Linnaeus 1758

GENOTYPE (by absolute tautonomy): *Concha pinna* Hasselquist 1757 (pre-Linnaean) = *Pinna muricata* Linnaeus 1758 (*fide* Grant & Gale 1931, 145). Recent, East Indies?

Pinna NEW SPECIES

PLATE 2, FIGURE 14

Pinna barrowsi Dickerson (1916) 431 (between Domengine and Cantua Creeks). Not *Pinna barrowsi* Dickerson (1914a) 125. *pl. 8, f. 3* (a Martinez species).

Figured specimen 32595; loc. 2287; (incomplete).

A single crushed individual representative of the genus *Pinna* occurs in the collections. The shell is elongate-cuneate, ornamented with 23 rounded radial ribs separated by interspaces of approximately equal width.

This species differs from *P. barrowsi* Dickerson in lacking concentric sculpturing, and from *P. lewisi* Waring in possessing strong radial sculpturing.

As figured, the specimen shows only a portion of the valve, as a segment approximately 14.0 mm. in width has been crushed back on the opposite side.

Family PTERIIDAE

Genus PTERIA Scopoli 1777

GENOTYPE (by monotypy): *Mytilus hirundo* Linnaeus. Recent, Mediterranean Sea.

Pteria pellucida (Gabb)

PLATE 2, FIGURES 1, 4, 7, 8

Avicula pellucida Gabb (1864) 186. *pl. 25, f. 172* (described).—Gabb (1869) 246 (Griswold's).—Dickerson (1916) 430, 444 (between Domengine and Cantua creeks).

? *Pteria clarki* Weaver & Palmer (1922) 12. *pl. 10, f. 5, 12, 15* (described, near Vader, Washington).

Lectotype 11983; Calif. State Survey Coll. no. 198; length (incomplete) 29.0 mm., altitude (incomplete) 22.4 mm.
Lecto-paratype 15576; Calif. State Survey Coll. no. 198; length 13.7 mm., altitude 12.0 mm.
Hypotype 32605; loc. A-975; length 25.0 mm., altitude 20.0 mm.
Hypotype 32623; loc. A-975; length (incomplete) 26.5 mm., altitude 25.0 mm.

Since Stewart's studies (1930), the type material of *Avicula pellucida* Gabb has been rediscovered in the collections of the Museum of Paleontology. As stated by Gabb the original figure was a synthetograph: "The outline is approximately restored from undulations on

a young specimen, the one figured being so decomposed as to show no lines of growth or other markings." Specimen no. 11983 corresponds both in size and outline with Gabb's figure, and is here designated the lectotype. The young specimen from which the growth-lines and the shape, ventrally and posteriorly, was restored is here designated as lecto-paratype no. 15576.

The lectotype is in a weathered brown sandstone of uncertain age; the lecto-paratype, in a dark gray sandstone filled with shell-fragments among which are *Turritella uvasana* subsp. and *Cylichna costata* Gabb, is almost certainly from the Domengine horizon at Martinez. The specific identity of a third specimen in the original material is open to question. It is an immature specimen of rather different proportions from the rest of the type material. It is possible that it is the "Chico" specimen mentioned by Gabb. The specimen upon which Gabb's record of the occurrence of this species at "Griswold's" is based has recently been found in the collections. It is labelled, presumably by Gabb, "Cretaceous B, Upper Beds, 10 miles W. of Griswold's."

Five specimens only occur in the collections from the Coalinga area. The line of the hinge and the anterior ear is straight, and the angle formed by lines drawn along the center of the umbonal ridge and the hinge-line varies from 41 to 49 degrees.

The specimen figured by Anderson & Hanna (1925: *pl. 1, f. 1*) as *Pteria pellucida* differs from Gabb's species in having the dorsal edge of the anterior ear at an angle to the hinge-line rather than forming a straight line, and in the umbonal ridge forming an angle of approximately 55 degrees with the hinge-line.

Genus EXPUTENS Clark 1934

GENOTYPE (here designated): *Exputens llajasensis* Clark. Eocene, Simi Valley, California.

Exputens alexi Clark

PLATE 2, FIGURES 2, 5, 9

Exputens alexi Clark (1934) 271. *pl. 37, f. 19–24* (described, loc. A-1007).

Holotype 32386; loc. A-1007; length 18.7 mm., altitude 13.1 mm.
Paratype 32385; loc. A-1007; length 19.0 mm., altitude 12.8 mm.
Paratype 32384; loc. A-1007; length 17.0 mm., altitude 12.0 mm.

Family PEDALIONIDAE

Genus PEDALION Huddesford 1770

GENOTYPE (by monotypy): *Ostrea isogonum* = ? error for *Ostrea isognomon* Linnaeus. Recent, Philippine Islands.

Iredale (1924: 190) has recently called attention to the use of *Pedalion* in Huddesford's edition of Lister, Linnaean Index. An examination of the reference indicates an unfortunate misinterpretation by Iredale, and the acceptance of *Pedalion* as of Huddesford is more complicated than one might wish. The Linnaean Index is arranged by Huddesford with the species listed on one page and the opposite page devoted to notes. Thus on page 22 under the heading "Ostrea," is to be noted as species 30 "Isogonum," while opposite on page 23 is noted "30. PEDALION. RUDDER. *Solander*." It is obvious that the names "Pedalion" and "Rudder" were considered as of similar nature, although Iredale appears to have interpreted "Rudder" as equivalent to "Solander" and presumably the name of some author. Both "Pedalion" and "Rudder" are in the same type face as "Ostrea," which heads page 22, and are presumably of generic nature. If "Pedalion" may be considered as a latinized generic name and "Rudder" as a vernacular name, it may be possible to retain the name *Pedalion* for the group of species which has long been known under this term.

It is rather unfortunate that the type species should be a somewhat aberrant form. The posterior ear is not characteristic of the majority of species referable to this genus. However, the type species of *Melina* Retzius 1788, and of *Perna* Bruguière 1789 (not *Perna* Retzius 1788), *Ostrea ephippium* Linnaeus, shows what is interpreted as the morphological development of such an ear, and the character may be too variable to be of systematic importance.

Ostrea ephippium was erroneously stated by Iredale to be the type of *Pedalion* Huddesford 1770. This species is no. 31 on the list, and the reference to *Pedalion* bears the number 30.

Pedalion joaquinensis NEW SPECIES

PLATE 2, FIGURES 3, 6, 10, 12, 15

Perna excavata "White"; Cooper in Watts (1894) 57 (San Joaquin Coal Mine).

Holotype 15577; loc. 7177; length 19.0 mm., altitude (incomplete) 20 0 mm.
Paratype 15578; loc. A-972; length 18.4 mm., altitude 26.0 mm.
Paratype 15579; loc. 7155; length 20.5 mm., altitude 25.0 mm.
Paratype 15580; loc. A-972; length 18.2 mm., altitude 24.5 mm.
Paratype 15581; loc. 7177; (incomplete).

DESCRIPTION.—Shell of medium size, compressed; dorsal margin straight, the posterior and ventral rounded, the anterior slightly concave; a small anterior ear angulate to the dorsal margin; umbos anterior, sharply prosogyrate; shell laminated, iridescent; surface smooth except for growth-lines; ligamental grooves four or five,

narrow-elongate, separated by interspaces equal in width to the grooves at the beak and becoming progressively wider posteriorly.

COMPARISON.—This species differs from *P. goniglensis* M. A. Hanna (1927: 275. *pl. 27, f. 12, 13, 14*) in lacking the deep anterior indentation characteristic of the San Diego species; the anterior margin, ventral to the byssal notch, does not project as far forward in the Coalinga species. The dorsal margin is never rounded, and the ear, characteristic of *P. joaquinensis*, is not well developed on *P. goniglensis.*

This species has been found only in the carbonaceous strata at the San Joaquin and California Coal Mines, northwest of Coalinga.

Family VULSELLIDAE

Genus VULSELLA (Bolten) Roeding 1798

GENOTYPE (by tautonomy): *Mya vulsella* Linnaeus. Recent, Red Sea.

The genus *Vulsella* is characterized by its ostreiform shape and external alivincular ligament set in an oblique triangular groove. It is represented in the Eocene of the Paris Basin, France, and according to Reeve (Conch. Icon. 11: "*Vulsella*") is most abundant in the modern fauna of the Red Sea.

Vulsella (?) clarki NEW SPECIES

PLATE 3, FIGURE 8

Ostrea sp. Dickerson (1916) 426, 431 (in part) (loc. 1817).

Holotype 15743; loc. 1817; length 20.3 mm., altitude 14.6 mm.

DESCRIPTION.—Shell ostreiform, moderately large, elongate posteriorly, inflated, attached; surface, other than area of attachment, marked by coarse lines of growth; ligamental groove external, elongate, triangular; shell thin at area of attachment, thick elsewhere; muscle-scar subcentral, moderately large.

COMPARISON.—*Vulsella* (?) *clarki* may be distinguished from all described West American species by its ostreiform shape and the external ligamental pit.

According to Reeve the genus occurs principally in association with sponges, and none of the figured species shows any indication of an area of attachment. The generic determination of the new species is therefore questioned, as a prominent area of attachment is visible on all the specimens in the collection.

One large specimen appears to have been attached to a large flat surface (possibly an *Aturia*) and, as a result, tends to be elongated ventrally rather than posteriorly.

Family OSTREIDAE

Genus OSTREA Linnaeus 1758

GENOTYPE (by subsequent designation, Children 1823): *Ostrea edulis* Linnaeus. Recent, coasts of Europe.

Ostrea idriaensis Gabb

Ostrea idriaensis Gabb (1869) 203, 252. *pl. 33, f. 103b, c, d; pl. 34, f. 103, a* (described, New Idria) —White (1884) *pl. 39, f. 7, 8* (after Gabb).—Turner & Stanton (1894) 95 (New Idria).—Cooper in Watts (1894) 57 (San Joaquin and California coal mines).—Stanton (1896) 1026 1027 (New Idria).—Anderson (1905) 166 (coal mines).—Arnold (1907) *pl. 9, f. 2* ("type" after Gabb).—Turner in Anderson (1908), 10 (New Idria).—Arnold (1909) 13. *pl. 2, f 4, 5* (northwest of Coalinga).—Arnold & Anderson (1910) 70. *pl. 24, f. 4, 5* (northwest of Coalinga).—Dickerson (1913) 265 (New Idria, Coalinga).—Dickerson (1916) 431, 446 (between Domengine and Cantua creeks).—Anderson & Hanna (1925) 191 (not at Tejon; described from vicinity of New Idria, Fresno County).—Clark in M. A. Hanna (1927) 260 (Coalinga).—Stewart (1930) 17 (New Idria), 126, 127 (synonymy). *pl. 8, f. 3; pl. 17, f. 1* (lectotype).—Vokes (1935a) 291–304. *pl. 22–24* (synonymy and variation).
? *Aucella piochii* Gabb; Cooper in Watts (1894) 57 (San Joaquin Coal Mine).
Ostrea columbiana Weaver & Palmer (1922) *pl. 8, f. 15, 16* (described, Coal Creek, Washington).
Ostrea oregonensis Packard (1923) 4. *pl. 1—4* (described, near Glide, Ore.).
Ostrea haleyi Hertlein (1933) 277. *pl. 18, f. 5, 6* (described, Domengine, Santa Rosa Island).

For a more complete discussion of this species than it is possible to give here, the reader is referred to an earlier paper by the writer (Vokes 1935a). *Ostrea idriaensis* is a brackish-water type, occurring only in the Vallecitos area in its normal development. Specimens from the vicinity of the San Joaquin and California coal mines, west of Coalinga, are typical in every way except that they never reach the size that is shown by the material from the type localities.

Small individuals, poorly preserved, are believed to be the basis of Cooper's record of *Aucella piochii*.

Ostrea idriaensis Gabb var. fettkei Weaver

PLATE 2, FIGURES 11, 13

Ostrea fettkei Weaver (1912) 30. *pl. 4, f. 37, 39* (described, Coal Creek, Washington).
Ostrea crandalli M. A. Hanna (1927) 275. *pl. 29, f. 1, 2* (described, La Jolla formation).
Ostrea idriaensis (? var.) *fettkei* Weaver; Vokes (1935a) 291.

Hypotype 15582; loc. A-1021; length 16.2 mm., altitude 24.8 mm.
Hypotype 15583; loc. A-1022; length (incomplete) 22.5 mm., altitude 31.2 mm.

As suggested in a footnote in an earlier paper by the writer, *Ostrea fettkei* Weaver represents a variety of *Ostrea idriaensis* bearing definite ribs which are of primary strength and not interrupted by the growth-

lines. Dr. Weaver's description was of the holotype of the variety, and an examination of specimens from the type locality and from the New Idria region indicates that there is no definite arrangement as to the strength of the ribbing on the surface of the shell. The specimens from the New Idria region are all larger than those from the Washington localities.

Ostrea aviculiformis Anderson

Ostrea aviculiformis Anderson (1905) 166, 194. *pl. 13, f. 3, 4, 5* (described, Avenal sands).—Arnold (1909) 13. *pl. 2, f. 12* (San Joaquin Coal Mine).—Arnold & Anderson (1910) 70. *pl. 24, f. 12* (San Joaquin Coal Mine).—Dickerson (1916) 431, 446 (Domengine Ranch).—Clark (1926) 115 (Coalinga).

The types of this species, described from the Avenal Sands, west and north of Coalinga, were recovered, considerably broken, after the San Francisco fire of 1906. Enough remains of the upper valve to indicate that it was strongly laminated, with laminae which were approximately one eighth of an inch apart. The upper portion, including the hinge area of the left valve, is present. Our collections from the Domengine north of Coalinga contain several specimens which are very similar in shape and outline to the left valve, but there are no right valves which show the prominent laminae indicated upon the fragment of the type which is preserved. These are therefore only tentatively referred to Anderson's species.

Ostrea NEW SPECIES

PLATE 3, FIGURE 5

Figured specimen 15744; loc. A-1308; length 72.0 mm., altitude 61.0 mm.

A single upper valve of a large *Ostrea* was collected in the Domengine formation near Los Gatos Creek by S. A. Berthiaume. The shell is thin with a superficial ornamentation of crude, low, rounded, divaricate radial ribbing. The visceral cavity is rather deep for an upper valve and has a large, subcentral muscle-scar. The ligamental area is small, almost flat, with two indistinct longitudinal ridges. The margin of the shell is crenulate internally.

Family PECTENIDAE

Genus PROPEAMUSSIUM de Gregorio 1884

GENOTYPE (by monotypy): *Pecten (Propeamussium) cecilae* de Gregorio. "Miocene," Sicily.

Propeamussium mideocenicum NEW SPECIES

PLATE 3, FIGURES 2, 3, 4

Pecten cf. *interradiatus* Gabb; Dickerson (1916) 426, 431 (loc. 1817).
Pecten vacavillensis "Palmer"; Merriam & Turner (1937) 94 (Lillis Ranch).

Syntype 15584; loc. 1817; length (incomplete) 9.5 mm., altitude 8.8 mm.
Syntype 15585; loc. 1817; length 6.1 mm., altitude 6.2 mm.
Syntype 15586; loc. 1817; length 7.5 mm., altitude 8.0 mm.

DESCRIPTION.—Shell small, thin, slightly higher than long; ventral margin evenly rounded, the anterior and posterior margins straight to the umbos; surface of left valve ornamented with 10 to 12 low, rounded ribs separated by flat-bottomed interspaces of varying width, widest on the center of the valve but never less than twice the width of the ribs; both ribs and interspaces marked by faint lines of growth; surface of right valve not seen; ears smooth, subequal, the byssal notch well-defined, small; interior of both valves with 10 to 12 ribs extending from the umbo to the ventral margin and directly opposite the ribbing on the exterior of the valve.

COMPARISON.—*Propeamussium mideocenicum* may be distinguished by the fact that the ribbing on the surface of the left valve is directly opposite that on the interior of the valve, which extends from the umbo to the ventral margin. *P. interradiatum* (Gabb*) has but 8 internal ribs which extend only half way down the valve from the umbo. *P. vacavillense* (Palmer†) also has but 8 internal ribs which occupy only the ventral two thirds of the valve. *P. lajollaense* (M. A. Hanna‡) from the La Jolla formation, has about 65 ribs on the exterior of the valve.

INCERTAE SEDIS

Pecten (?) NEW SPECIES

PLATE 3, FIGURE 1

Figured specimen 15601; loc. A-1012; length 4.2 mm., altitude 5.0 mm.

A single crushed left (?) valve of a small species of *Pecten* (?) occurs in the collections from the Vallecitos. There are 16 or 17 radial ribs which pass from the apex to the ventral margin, and alternating finer inter-ribs which extend from the ventral margin approximately two thirds of the distance to the apex. The posterior ear is ornamented by 7+ fine radiating ribs; the anterior ear is missing. The ribbing appears on the inner side of the valve as grooves. The interspaces between the ribs and the inter-ribs are as wide as the ribs.

Family SPONDYLIDAE

Genus SPONDYLUS Linnaeus 1758

GENOTYPE (by subsequent designation, Gray 1847): *Spondylus gaederopus* Linnaeus. Recent, Mediterranean Sea.

* Gabb (1869) 199. *pl. 33, f. 98, 98a;* as *Pecten interradiatus.*
† Palmer (1923) 301. *pl. 55, f. 3, 4a, 4b, 5;* as *Pecten vacavillensis.*
‡ M. A. Hanna (1927) 277. *pl 32, f. 1, 3, 4, 5, 6;* as *Pecten lajollaensis.*

Spondylus carlosensis Anderson

PLATE 3, FIGURES 10, 13

Spondylus carlosensis Anderson (1905) *pl. 13, f. 1* (west and north of Coalinga, described).—Arnold (1909) 13, *pl. 2, f. 6, 7* (northwest of Coalinga).—Arnold & Anderson (1910) 70. *pl. 24, f. 6, 7* (northwest of Coalinga).—Dickerson (1916) 431, 447 (between Domengine and Cantua creeks).—Anderson & Hanna (1925) 189, 190 (described from Coalinga).—Clark (1926) 115 (Coalinga).

Hypotype 32708; loc. 2293; length (incomplete) 35.0 mm., altitude (incomplete) 34.5 mm.

The left valve figured is irregular in outline. There is a well-marked regular umbonal area of development during the period preceding attachment. The sculpture consists of irregular, sharp, round-topped ribs of varying strength, usually large ribs alternating with smaller ones, with approximately nine more prominent noded ribs subequally spaced over the surface of the valve. The ears have been broken.

The hinge shows long auricular crurae, buttressed ventrally by two ridges. The ligamental groove is long and narrow, extending to the apex; the crural sockets are subtriangular, set beneath the umbonal ends of the crurae. The hinge figured by Anderson & Hanna (1925: *text-f. 10*) shows none of the characters of the genus and is wholly unsatisfactory for purposes of identification.

Spondylus cliffensis M. A. Hanna (1927: 278. *pl. 32, f. 2, 7*)* is a smaller species and appears to be characterized by the possession of a longer hinge-line.

Family ANOMIIDAE

Genus PODODESMUS Philippi 1837

GENOTYPE (by monotypy): *Pododesmus decipiens* Philippi = *Placumanomia rudis* Broderip. Recent, Cuba.

Subgenus MONIA Gray 1849

TYPE SPECIES (by subsequent designation, Bucquoy, Dautzenberg, & Dollfus 1888): *Anomia zealandica* Gray. Recent, New Zealand.

Pododesmus (Monia) inornatus (Gabb)

PLATE 3, FIGURES 6, 7, 9, 11

Placunanomia inornata Gabb (1864) 217. *pl. 32, f. 288, a* (described, Corral Hollow).—Anderson (1905) 166 (north of Coalinga).—Arnold (1909) 13 (Zapatos Creek), 16. *pl. 3, f. 1* (northwest of Coalinga).—Arnold & Anderson (1910) 70. *pl. 25, f. 1. 10.*—Dickerson (1916) 431 (between Domengine and Cantua creeks).

? *Anomia mcgoniglensis* M. A. Hanna (1927) 278. *pl. 31, f. 1, 2, 5, 7* (described, La Jolla formation).

Hypotype 15587; loc. A-1312; length 18.5 mm., altitude 20.6 mm.
Hypotype 15588; loc. A-1312; length 17.5 mm., altitude 20.4 mm.
Hypotype 15589; loc. A-1101; length 25.5 mm., altitude 21.5 mm.
Hypotype 15590; loc. A-1101; length 22.0 mm., altitude 19.8 mm.

---

* La Jolla formation.

Recent collections from Corral Hollow have furnished abundant material representing Gabb's species. Among the specimens is a right valve through the byssal notch of which projects a portion of a somewhat calcified byssus. There is a single prominent muscle-scar on the disk. The valve embraces but does not join about the foramen, which is bordered posteriorly by the ventral buttress of the posterior ligamental platform. The right valve is flattened; the left moderately to well inflated. The umbos are prominent, and there is a well developed cardinal area.

The Domengine specimens show a range in coarseness of sculpturing which fully embraces both Gabb's and Hanna's species. The interior of *Anomia mcgoniglensis* is not sufficiently well known to allow determination of its true generic position.

Family MYTILIDAE

Genus MYTILUS Linnaeus 1758

GENOTYPE (by subsequent designation, Anton 1839): *Mytilus edulis* Linnaeus. Recent, world-wide distribution.

Mytilus dichotomus Cooper

PLATE 3, FIGURE 14

Modiola cylindrica "Gabb"; Cooper in Watts (1894) 56 (San Joaquin Coal Mine).
Mytilus quadratus "Gabb"; Cooper in Watts (1894) 57 (California Coal Mine).
Mytilus dichotomus Cooper (1894) 49. *pl. 5, f. 64* (described, California Coal Mine).—Anderson & Hanna (1925) 187 (compared to *Septifer dichotomus* Gabb).—Stewart (1930) 101, 102 (? = *Brachidontes cowlitzensis*).
Septifer dichotomus "Gabb;" Arnold (1909) 13. *pl. 2, f. 3* (San Joaquin and California coal mines).—Arnold & Anderson (1910) 70. *pl. 24, f. 3* (San Joaquin and California coal mines).

Hypotype 15592; loc. A-1017; length 12.5 mm., altitude 26.5 mm.

This species was described from "the headwall of the California Coal Mine, Huron, Fresno County," as being very similar to *Septifer dichotomus* Gabb, but without any trace of a septum inside the beaks.

Cooper thought it probable that this species was congeneric with *Septifer dichotomus* Gabb, that Gabb was mistaken in his generic determination. Therefore he proposed the same specific name so that if Gabb's generic determination proved incorrect there would be little confusion. A specimen in the collections of the University of California labelled *Septifer dichotomus* Gabb from the Tejon agrees with the original figure in size and shape and is presumably the holotype of that species. It is certainly a *Septifer*, and the form described by Cooper is distinct and differs from Gabb's species in having much finer sculpturing.

It appears to be certain that some forms identified as *Septifer dichotomus* are in reality *Mytilus*. Arnold's figure has lost the anterior end, but the locality given is the San Joaquin Coal Mine, where *Mytilus dichotomus* is abundant and from which no specimens of *Septifer dichotomus* have been obtained by the writer.

Mytilus (?) NEW SPECIES

PLATE 3, FIGURE 12

Figured specimen 15591; loc. A-1168; length 36.0 mm., altitude 55.0 mm.

A single poorly preserved left valve of a large *Mytilus*-like form is in the collection. The dorsal edge is straight; the ventral edge broadly rounded, somewhat angulate at the posterior ventral margin; posterior end rounded to the dorsal margin. There is no indication of any surface ornamentation, the evidence suggesting that none existed. The ligamental area was long, including the greater length of the dorsal margin.

No similar form has been described from West American deposits, but the nature of the preservation has prohibited an adequate description of the present material.

Genus BRACHIDONTES Swainson 1840

GENOTYPE (by monotypy): *Brachidontes sulcata* = ? *Brachidontes modiolus* (Linnaeus), *fide* Hanley, 1855. Recent, Indian Ocean.

Most paleontologists have spelled this generic name "*Brachydontes*," following Gray (1847: 199).

Brachidontes cf. cowlitzensis (Weaver & Palmer)

Modiola ornata Gabb (1864) 184, 234. *pl. 24, f. 166* (described).—Gabb (1869) 245 (Griswold's, New Idria).—Turner & Stanton (1894) 95 (New Idria).—Stanton (1896) 1026, 1027 (New Idria).—Anderson (1905) 166 (north of Coalinga).—Turner in Anderson (1908) 11 (New Idria).

Modiolus ornatus "Gabb"; Anderson in Dumble (1912) 32 (Salt Creek and Coalinga).—Dickerson (1916) 426, 427, 431, 446 (between Domengine and Cantua creeks).—Clark (1921) 138, 158 ("Meganos," north of Coalinga). Not *Mytilus ornatus* Orbigny (1844) 283. *pl. 342, f. 10–12* (= *Brachidontes*).

Cf. *Modiolus* (*Brachydontes*) *cowlitzensis* Weaver & Palmer (1922) 16. *pl. 9, f. 19* (described, near Vader, Washington).

? *Modiolus kelsoensis* Weaver & Palmer (1922) 17. *pl. 10, f. 13* (described, Coal Creek, Washington).

? *Modiolus columbianus* Weaver & Palmer (1922) 17. *pl. 8, f. 7* (described, Coal Creek, Washington).

? *Modiolus lawsoni* Nelson (1925) 408. *pl. 50, f. 3, 4* (described, Simi Valley).

Modiolus (*Brachydontes*) *ornatus* Gabb; Clark (1926) 114 (Coalinga).—Clark & Woodford (1927) 89. *pl. 14, f. 10* (ranges throughout the California Eocene).

Brachidontes cowlitzensis ? Stewart (1930) 100–102 (synonymy).

Gabb's original figure shows the area anterior to the beaks ornamented as is the rest of the shell; the specimens of *Brachidontes cowlitzensis* available for study show the same condition, although somewhat variable as to the strength of the development of the ribs. In nearly all the specimens from the Domengine and Capay horizons this ribbing is so obsolete as to present an almost smooth surface. In no case is the outline and prominence of the umbonal ridge constant.

This species is rare in all horizons of the Domengine formation, but is abundant at loc. 1817 in the Arroyo Hondo formation.

Order ANOMALODESMACEA

Family PERIPLOMATIDAE

Genus PERIPLOMA Schumacher 1817

GENOTYPE (by monotypy): *Periploma inaequivalvis* Schumacher. Recent.

Periploma eodiscus NEW SPECIES

PLATE 4, FIGURES 1, 3

Syntype 15595; loc. 4178; length 20.5 mm., altitude 16.2 mm.
Syntype 15596; loc. 4178; length 22.0 mm., altitude 19.8 mm.

DESCRIPTION.—Valves discrepant, the right slightly more inflated than the left; shell elongate-ovate, thin; umbo subcentral, opisthogyrate, prominent; anterior and ventral margin rounded, the posterior produced, the dorsal straight; surface with two shallow grooves on the posterior portion of the left valve and a corresponding wide, low ridge on the right valve; sculpture mainly of lines of growth with a few low, broad, concentric undulations, which are most prominently developed in the grooves on the left valve; interior not seen.

COMPARISON.—This species most closely resembles *P. discus* Stearns,* from which it differs in being longer in proportion to its height, in having a shorter straight dorsal margin, in lacking the anterior grooved undulation on the right valve, and in being less produced posteriorly in the right valve. It differs from *P. stewartvillensis* Clark & Woodford (1927: 89. *pl. 14, f. 11*) in shape, in being less inflated, and in possessing concentric undulations on the surface of the valve.

Two specimens only, the types, found in the upper sandy shales of the Arroyo Hondo formation in the vicinity of Domengine Creek.

* Stearns (1890) 222. *pl. 16, f. 1, 2.* Not *P. discus* Gardner (1926a) 61. *pl. 15, f. 11–13* (Shoal River formation, Florida); renamed *P. gardnerae* ("*gardneri*") Soot-Ryan (1932) 10.

Family CUSPIDARIIDAE

Genus CARDIOMYA A. Adams 1864

GENOTYPE (by monotypy): *Neaera gouldiana* Hinds. Recent, Japanese seas.

The species referred to the genus *Cardiomya* A. Adams differ from those referred to *Cuspidaria* Nardo in possessing prominent radial sculpturing on the surface of the valve.

Cardiomya turneri NEW SPECIES

PLATE 4, FIGURE 9

Cardiomya dolabraeformis "(Gabb)"; Stewart (1930) 308, 309 (in part). *pl. 7, f. 2.* Not *Neaera dolabraeformis* Gabb (1864) 153, 230 *pl. 22, f. 125.*

Holotype 15597; loc. A-1027; length 5.2 mm., altitude 3.2 mm.

DESCRIPTION.—Shell small, inflated; umbos prominent, almost central to the full length of the shell, decidedly posterior to the expanded area; anterior portion of the shell distinctly subangulate, forming an anterior slope which is smooth and devoid of ribbing; the rest of the surface of the expanded area sculptured by 14 radiating ribs and by prominent lines of growth; the posterior 8 ribs larger and more widely spaced than those on the anterior portion of the valve, and bearing between the third and fourth ribs from the posterior end a smaller inter-rib; rostrum forming slightly more than one third of the length of the shell, well developed and devoid of ribbing.

COMPARISON.—*C. turneri* differs from *C. dolabraeformis* in shape, the expanded portion of the shell in *C. turneri* being approximately as high as long, and in *C. dolabraeformis* only about three fourths as high as long; and in the character of the ribbing, which, so far as visible on *C. dolabraeformis*, is of approximately equal strength over the surface of the expanded portion of the shell, with well-developed inter-ribs between the posterior ribs. It differs from *C. comstockensis* Turner* *C. israelskyi* (M. A. Hanna†), *C. russelli* (M. A. Hanna‡), and *C. vorbei* (M. A. Hanna§) in the absence of radiating ribs on the rostrum, which is relatively broader and shorter than on *C. russelli.*

Named in honor of Dr. F. E. Turner of the Texas Agricultural and Mechanical College.

The holotype of *Neaera dolabraeformis* Gabb is in the Univ. Calif. Mus. Paleont. Collections, no. 11991, and is here figured (PLATE 4,

---

* Turner (1938) 47. *pl. 8, f. 8.*

† M. A. Hanna (1927) 280. *pl. 34, f. 1, 5;* as *Cuspidaria israelskyi.*

‡ M. A. Hanna (1927) 280. *pl. 34, f. 8;* as *Cuspidaria russelli.*

§ M. A. Hanna (1927) 281. *pl. 34, f. 4;* as *Cuspidaria vorbei.*

FIGURE 2). It is a poorly preserved specimen with only a part of the original shell present. This bears 11 radiating ribs and the internal cast of the shell indicates that there were approximately 9 more ribs. Between the first and second, the fourth and fifth, and the fifth and sixth ribs from the posterior end are well-developed inter-ribs. The rostrum is broken and worn but there is a suggestion of radial ribbing.

The matrix is the coarse brown sandstone which, together with the preservation, is characteristic of the Martinez formation, and there can be little doubt that Dickerson (1914a: 108, 112, 151. *pl. 9, f. 9*) was correct in reporting this as a Martinez species.

Cardiomya domenginica NEW SPECIES

PLATE 4, FIGURE 5

Holotype 15598; loc. A-1027; length 4.8 mm., altitude 3.0 mm.

DESCRIPTION.—Shell small, moderately inflated; umbos prominent, heavy, subcentral; rostrum short, small, smooth; disk with 14 equally developed radial threads which are separated by interspaces of equal width; anterior dorsal slope smooth and devoid of ribbing; interior not seen.

COMPARISON.—*C. domenginica* may be separated from all the described smoothly rostrate species by the possession of radial threads which are all of equal strength and are separated by interspaces of equal width, with no indication of the development of inter-ribs.

Cardiomya silverensis NEW SPECIES

PLATE 4, FIGURE 7

Holotype 15599: loc. A-1027; length 4.1 mm., altitude 2.9 mm.

DESCRIPTION.—Shell small, inflated; umbos high, prominent, centrally located on the expanded portion of the valve; disk with 18 elevated radial threads, the posterior 7 of which are more strongly developed and farther apart than the anterior 11, all of the ribbing decidedly curved posteriorly; rostrum short, stout, subtruncate, with 3 well-developed radial threads extending from the umbo to the center and the ventral margins at its posterior extremity, and with 2 threads along the dorsal margin.

COMPARISON.—*C. silverensis* differs from *C. turneri* and *C. domenginica* in the presence of radial ribbing on the rostrum. *C. russelli* has a more elongate, narrower rostrum, which bears but one radial thread; *C. israelskyi*, *C. vorbei* and *C. comstockensis* differ in the number

and comparative strength of the ribbing on the disk, and in the shape and number of ribs on the rostrum.

Named for its occurrence at U. C. loc. A-1027 near Silver Creek on the north-east side of the Vallecitos syncline.

Cardiomya NEW SPECIES

PLATE 4, FIGURE 11

Figured specimen 15600; loc. 1817; length (incomplete) 4.5 mm., altitude (incomplete) 3.0 mm.

A single broken left valve of a *Cardiomya* occurs in the collections from the Capay stage. The preserved surface is sculptured by 17 radial ribs, which are most strongly developed posteriorly and become progressively weaker toward the anterior end of the valve. Alternating with almost all of the ribs are well-developed inter-ribs. The rostrum was well developed and apparently smooth.

The presence of an inter-rib between the major radial ribs on both the anterior and posterior portions of the valve differentiates this form from all described West Coast Eocene species.

Order TELEODESMACEA

Family CRASSATELLIDAE

Genus CRASSATELLA Lamarck 1799

GENOTYPE (by monotypy): *Crassatella gibba* Lamarck 1801 = *C. tumida* Lamarck 1807 = *Venus ponderosa* Gmelin (*fide* Stewart 1930). Eocene, Paris Basin, France.

Crassatella mulates (M. A. Hanna)

PLATE 4, FIGURES 14, 15

Crassatellites mulates M. A. Hanna (1927) 282. *pl. 34, f. 2, 3, 6, 7, 9* (described, La Jolla formation).

Hypotype 30621; loc. 3958; length 44.0 mm., altitude 42.0 mm.
Hypotype 30623; loc. 3958; length 46.0 mm., altitude 43.0 mm.

In Hanna's figure of the type specimen some matrix present on the posterior extremity of the specimen has resulted in giving it a more rounded appearance than is actually the case. Specimens from the Coalinga region, better preserved than the type, show a straight posterior margin. The species may be distinguished by this straight posterior margin and by the posterior angulation of the surface of the shell.

Crassatella cf. meganosensis (Clark & Woodford)

PLATE 4, FIGURE 13

Cf. *Crassatellites meganosensis* Clark & Woodford (1927) 82, 90. *pl. 15, f. 1, 2, 3, 4, 5* (described, Meganos formation).

Hypotype 30622; loc. 2292; length 52.0 mm., altitude 43.1 mm.

Two right valves referable to this species occur in the collections. They differ from the typical *C. meganosensis* in having the beak more anterior, and the posterior angulation is not so well developed. There is a definite, fairly large escutcheon. The type of *C. meganosensis* is a left valve and has a small, poorly defined escutcheon. The escutcheon in *Crassatella* is in many cases unequally divided between the two valves, and this appears to be the condition in *C. meganosensis.*

C. mulates has a straighter posterior margin, a sharper posterior angulation, and is higher in proportion to the length of the shell.

Crassatella uvasana (Conrad) semidentata (Cooper)

PLATE 4, FIGURES 4, 6, 8, 10, 12

Astarte semidentata Cooper (1894) 48. *pl. 3, f. 44, 45* (described, San Diego).—Dickerson (1916) 430 (between Domengine and Cantua creeks).
Crassatellites grandis (Gabb); Arnold (1909) 13. *pl. 2, f. 10, 10a; pl. 3, f. 14* (north of Coalinga).—Arnold & Anderson (1910) 70. *pl. 24, f. 10, 10a; pl. 25, f. 14* (north of Coalinga).—Dickerson (1916) 430, 444 (between Domengine and Cantua creeks).
Crassatellites uvasana (Gabb); Dickerson (1916) 430 (between Domengine and Cantua creeks).
Crassatellites mathewsonii (Gabb); Dickerson (1916) 430, 444. *pl. 36, f. 9a, 9b* (loc. 672).
Crassatellites (Astarte) mathewsonii (Gabb); Dickerson (1916) 462 (near Domengine Creek).

Hypotype 11798; loc. 672; length 12.7 mm., altitude 11.4 mm.
Hypotype 15624; loc. 672; length (incomplete) 18.3 mm., altitude 17.0 mm.
Hypotype 15602; loc. 2291; length 30.5 mm., altitude (incomplete) 26.0 mm.
Hypotype 15603; loc. 2292; length 33.3 mm., altitude 30.0 mm.
Hypotype 15604; loc. A-1219; length 45.0 mm., altitude (incomplete) 42.4 mm.

As shown by Turner,* the forms of the *C. uvasana* group are most satisfactorily identified by the character of the umbos, which reflect the condition of the young shell. In *C. uvasana semidentata* the young shell is comparatively tall. Upon attaining a magnitude of approximately seven millimeters the rate of growth on the posterior margin appears to have increased, tending to produce a concavity at that point, and giving the umbo an attenuated appearance. The concentric ribbing on the young shell is finer, more regular, and seemingly more persistent than on *C. uvasana uvasana.*

Coalinga appears to represent a northern limit for this subspecies. In the Domengine in the vicinity of Martinez and in Oregon the subspecies *C. uvasana mathewsonii* is present. This suggests that *C. uvasana*

* Turner (1938) 47, 48.

mathewsonii is a northern form, and *C .uvasana semidentata* a southern form whose range may have been controlled by temperature conditions.

Family SPHAERIIDAE

Genus CORBICULA Megerle 1811

GENOTYPE (by monotypy): *Corbicula fluminalis* Megerle = *Tellina fluminalis* Muller. Recent, mouth of Euphrates River.

Corbicula carlosensis NEW SPECIES

PLATE 5, FIGURES 1, 2, 3, 4, 5, 6

Corbicula sp. Stanton (1896) 1027 (New Idria).

Holotype 15605; loc. A-1028; length 19.6 mm., altitude 17.2 mm.
Paratype 15606; loc. A-1028; length 18.5 mm., altitude (incomplete) 17.8 mm.
Paratype 15607; loc. A-1028; length 20.2 mm., altitude 17.8 mm.
Paratype 15608; loc. A-1028; length (incomplete) 18.6 mm., altitude 19.3 mm.
Paratype 15609; loc. A-1110; (incomplete).
Paratype 15610; loc. A-1110; (incomplete).

DESCRIPTION.—Shell variable, subcircular to subtriangular in outline; umbos central, inflated, prominent; anterior and posterior dorsal margins straight; anterior, ventral, and posterior margins broadly and regularly rounded; surface with a faint inconspicuous posterior umbonal ridge, and an ornamentation of coarse, concentric lines of growth; hinge with three well-developed cardinal teeth, and prominently cross-striated anterior and posterior laterals.

COMPARISON.—*C. carlosensis* may be distinguished from *C. eufaulaensis* Weaver* (and its synonym *C. cowlitzensis* Weaver†) in the possession of an umbonal ridge. *C. williamsoni* Anderson & Hanna‡ has a much smaller and weaker hinge-plate, and is strongly produced posteriorly.

Family CARDITIDAE

Genus VENERICARDIA Lamarck 1801

GENOTYPE (by subsequent designation, Schmidt 1818): *Venericardia imbricata* Lamarck = *Venus imbricata* Gmelin. Eocene, Paris Basin, France.

Subgenus GLYPTOACTIS Stewart 1930

TYPE SPECIES (by original designation): *Venericardia hadra* Dall. Chipola, Miocene, Florida.

* Weaver (1912) 32. *pl. 14, f. 119; pl. 15, f. 131.*
† Weaver (1912) 33. *pl. 14, f. 117; pl. 15, f. 132, 135.*
‡ Anderson & Hanna (1925) 164. *pl. 1, f. 4; pl. 3, f. 2.*

Venericardia (Glyptoactis ?) domenginica NEW SPECIES

PLATE 5, FIGURES 7, 8, 9

Venericardia "*alticostata* Gabb"; Arnold (1909) 13 (south of Los Gatos Creek).—Arnold & Anderson (1910) 70 (south of Los Gatos Creek).
Venericardia alticosta "Gabb"; Arnold (1909) *pl. 3, f. 12* (south of Los Gatos Creek).—Arnold & Anderson (1910) *pl. 25, f. 12* (south of Los Gatos Creek). Not ? *Cardita alticosta* Gabb (1869) 268. *pl. 36, f. 16* (a Mexican species).

Holotype 15611; loc. A-1219; length 24.5 mm., altitude 24.0 mm.
Paratype 15612; loc. A-1003 (Pine Canyon, Mt. Diablo); length 19.2 mm., altitude 19.0 mm.
Paratype 15613; loc. A-1003; length 14.5 mm., altitude 14.1 mm.

DESCRIPTION.—Shell small, moderately inflated, inequilateral, almost circular in outline; umbo small, high, prominent; lunule impressed; sculpture consisting of 17 radial, ridged, strongly beaded ribs, separated by round-bottomed interspaces slightly more than half as wide as the ribs, the ribs being finer and closer together on the posterior portion of the valve; posterior cardinal of the hinge in the right valve long, slender, curved, the anterior cardinal in the left valve reduced to a small rugosity bounding the anterior end of the large central socket, with a well-defined anterior lateral pustule.

COMPARISON.—*V. domenginica* differs from all the described western Eocene species referred to the *Carditidae* in size, shape, and character of the ribbing. It finds its nearest analogue in the group of *V. acuticostata* in the Lutetian-Bartonian of France.

These small species of *Venericardia* have not heretofore been studied in the California Eocene. Previous writers have apparently considered them to represent immature individuals of the larger described species, here referred to the genus *Megacardita* Sacco. They differ from these in possessing a well-developed anterior lateral tooth. Forms similar to *V. domenginica* have been found in the collections from the type Tejon, the Llajas formation, and the Eocene in the vicinity of Mount Diablo.

Genus MEGACARDITA Sacco 1899

GENOTYPE (by monotypy): *Venericardia jouanneti* Basterot. Helvetian, Tortonien, Europe.

The species here included as *Megacardita* have previously been classified as belonging to the genus *Venericardia* Lamarck. The type of *Venericardia* is *V. imbricata* (Gmelin). As figured by Cossman & Pissarro (1906: *pl. 31, f. 97-4*) this species has a genetic tendency toward the possession of a small anterior lateral tooth and has a smaller lunule than is found in the Eocene species from western America that have been referred to the genus *Venericardia*. *Megacardita* is char-

acterized by the absence of the anterior lateral and by the presence of a lunule which tends to be compressed. The ribbing is strong and smooth, while that of *V. imbricata* is rounded and strongly marked by imbricate, folliaceous scales.

Subgenus VENERICOR Stewart 1930

TYPE SPECIES (by original designation): *Venericardia planicosta* Lamarck. Eocene, Paris Basin, France.

Typical *Megacardita* shows a longer ligamental area than is characteristic of the Eocene species; also, as figured by Cossmann & Peyrot (1912: *pl. 3, f. 1–4*), the right anterior cardinal is seen to be sharply curved dorsally, a condition which is not seen in *Venericor*.

Megacardita (Venericor) vallecitosensis NEW SPECIES

PLATE 5, FIGURES 10, 11, 12

Holotype 15614; loc. A-1022; length 65.0 mm., altitude 63.0 mm.
Paratype 15615; loc. A-1022; length 32.5 mm., altitude 31.5 mm.

DESCRIPTION.—Shell large, heavy, almost circular in outline; umbos moderately inflated; surface with 23 radiating ribs, those on the central portion of the valve being planicostate and separated by flat-bottomed interspaces about two thirds as wide as the ribs; valve slightly angulate at the sixth rib from the posterior margin, the posterior ribs narrow, somewhat ridged and closer together, the anterior 5 or 6 ribs so interrupted by the growth-lines as to appear to be noded, and separated by interspaces wider than the ribs; growth-lines elsewhere on the shell not prominent; lunule small and inconspicuous; hinge-plate small, the central cardinal of the left valve comparatively small, trigonal in shape and somewhat posterior to the umbo; socket large, curved on both the anterior and posterior sides; posterior cardinal long, thin, and high; nymph-plate thin, high, so close to the posterior cardinal as to suggest a deeply grooved tooth.

COMPARISON.—*M. vallecitosensis* may be readily separated from all previously described West American species by the flat-topped ribbing, which more nearly approaches the type characteristic of *M. planicosta* than is the case in any other recognized species from this region.

Megacardita (Venericor) aragonia (Arnold & Hannibal) smileyi NEW SUBSPECIES

PLATE 6, FIGURES 1, 2, 3

Venericardia planicosta hornii "Gabb;" Dickerson (1916) 432 (loc. 672).

Holotype 15626; loc. 672; length 86.5 mm., altitude 78.0 mm.
Paratype 15627; loc. 672; (incomplete).

DESCRIPTION.—Shell large, heavy, with prominent umbos; posterior broadly rounded from umbo to posterior ventral edge where quite angulate, the ventral margin broadly rounded to the anterior cardinal edge, the shell there rounding sharply to the straight anterior cardinal margin; lunule small, deeply impressed; escutcheon elongate, well developed; surface with 21 rounded subobsolete ribs separated by narrow linear interspaces, the posterior 5 ribs narrower and less well developed than those on the rest of the valve; right valve of the hinge with a large trigonal and curved cardinal; left valve with a small elongate anterior cardinal and an elongate curved posterior cardinal, the posterior cardinal broad ventrally.

COMPARISON.—This subspecies may be distinguished from *M. aragonia* (Arnold & Hannibal*) by the stronger ribbing. In specimens of size equivalent to that of the holotype of the subspecies *smileyi* the ribbing is totally obsolete. The large trigonal cardinal in the right valve of this subspecies also differs greatly from the narrow elongate cardinal in *M. aragonia.* The size of this cardinal is quite variable in the latter species, but in none of the specimens examined does it approach the size or the trigonal outline which is characteristic of the Coalinga subspecies. The details of the outline serve to separate this form from any of the other described species from the West Coast Eocene.

Named in honor of Doctor F. J. Smiley, Professor of Geology at Occidental College, Los Angeles.

Megacardita (Venericor) hornii (Gabb) carlosensis NEW SUBSPECIES

PLATE 7, FIGURES 1, 2, 3, 4, 5, 6

Cardita hornii Gabb (1869) 187, 243 (New Idria). Not *C. hornii* Gabb (1864).

Holotype 15619; loc. A-1017; length 73.0 mm., altitude 57.5 mm.
Paratype 15620; loc. A-1017; length (incomplete) 67.0 mm., altitude 63.6 mm.
Paratype 15621; loc. A-1017; length (incomplete) 51.0 mm., altitude 45.7 mm.
Paratype 15622; loc. A-1017; length (incomplete) 30.5 mm., altitude (incomplete) 23.0 mm.

DESCRIPTION.—Shell moderately large, thin for the genus, variable in shape, quadrate to subtrigonal; umbos small, anterior; lunule minute, deeply impressed; escutcheon narrow, elongate; posterior end of shell obliquely angulate; surface with 21 radial ribs, the posterior 5 ribs small, rounded and weakly developed, separated by interspaces of equal width; the 3 ribs anterior to these strongly developed, persistently flat-topped, angulate at the edges, and separated by V-shaped

* Arnold & Hannibal (1914) 907; as *Venericardia aragonia.*

interspaces of equal width; the 5 anterior ribs nodose in appearance due to the strength of the growth-lines and separated by interspaces of equal width; the 8 ribs on the center of the valve minutely nodose in the early stages of development, flat-topped during adolescence, and rounded in the adult; hinge-plate small, the right cardinal curved, narrow and elongate, the nymph-plate long and grooved, the right socket narrow and obliquely set with a small tubercle on the anterior side; the left anterior cardinal small and subtriangular, the posterior cardinal long, thin, and curved, the nymph-plate long, low, and so closely set against the posterior cardinal as to appear to be a part of that tooth.

COMPARISON.—The small umbo and general outline is very suggestive of Gabb's original figure of *M. hornii*, but the small hinge-plate with the narrow elongate right cardinal, and the character of the ribbing are distinctive. The shape and the character of the ribbing is sufficient to distinguish the new subspecies from all other described species of *Megacardita.*

ADDITIONAL NOTES.—The number of ribs is constant: of 40 specimens examined 4 had 20 ribs, 27 had 21, 8 had 22, and 1 had 23. This form occurs at but one locality in the Vallecitos (U. C. loc. A-1017), where it is associated with *Pelecyora aequilateralis* (Gabb), *Ostrea idriaensis* Gabb, *Loxotrema turrita* Gabb, *Potamides carbonicola* Cooper, and *Calyptraea diegoana* (Conrad). These species suggest that the water was of less than normal salinity, which may be a possible explanation for the thin shell and the great variation in shape.

Megacardita (Venericor) hornii (Gabb) joaquinensis NEW SUBSPECIES

PLATE 8, FIGURES 1, 2; PLATE 9, FIGURES 1, 2

Cardita horni Gabb (*C. planicosta* Conrad); Anderson (1905) 164 (Avenal sandstones).

Holotype 15616; loc. 4170; length 110.4 mm., altitude 96.0 mm.
Paratype 15617; loc. 4169; length 100.5 mm., altitude 86.0 mm.
Paratype 15618; loc. A-819; length 105.5 mm., altitude 83.5 mm.

DESCRIPTION.—Shell large, heavy, variable in shape; umbos prominent, inflated, anterior; posterior cardinal margin convex, rounded, ventral nearly straight, anterior broadly rounded ventrally but quite sharply rounded dorsally, straightening out to the small, deeply impressed lunule; sculpture consisting of 21 subobsolete radial ribs appearing as low rounded waves on an otherwise smooth surface; hinge-plate large; posterior cardinal on the left valve long, thin, strongly

curved; anterior cardinal short, thin, small; nymph-plate strong, appressed to the posterior cardinal at the anterior end.

COMPARISON.—This subspecies may be distinguished from typical *M. hornii* (Gabb*) and *M. hornii clarki* (Weaver & Palmer†) by the obsolete character of the ribbing. It differs from *M. aragonia* (Arnold & Hannibal‡) in being less angulate at the posterior ventral margin, more sharply rounded anteriorly, and in having lower, more massive umbos. It differs from other described forms of *Megacardita* in both shape and character of ribbing.

The principle variation in this species is in the height-length ratio. The general features of the outline, notably the shape of the anterior and posterior ends, are constant and appear to be characteristic. The subspecies is confined to the collections from the Reef Ridge area and is notably abundant in the chert-pebble conglomerate at the base of the section in that area.

Megacardita (Venericor) hornii (Gabb) cf. calafia (Stewart)

Cardita hornii Gabb (1869) 188, 243 (Griswold's). Not *C. hornii* Gabb (1864).
Cf. *Venericardia hornii calafia* Stewart (1930) 168. *pl. 11, f. 2* (described, Simi Valley).

Specimens of a large *Megacardita* collected by Gabb from "10 miles W. of Griswold's, Cretaceous, Division B, Upper Beds" are provisionally referred to Stewart's subspecies. There are 24 radial ribs, obsolete upon the adult, but the anterior end does not appear to be as well rounded nor as high as is the case in the specimens from the Simi Valley.

Megacardita SPECIES

Venericardia planicosta hornii "(Gabb)"; Dickerson (1916) 426, 427, 432 (loc. 1817).

Poorly preserved and incomplete specimens of a rather small species of *Megacardita* occur in the collections from locality 1817. The ribs are rounded and separated by linear interspaces. The number of ribs and the details of the outline are not determinable, and the specimens serve only to record the presence of the genus in this horizon north of Coalinga.

Family LUCINIDAE

Genus LUCINA Bruguière 1797

GENOTYPE (by subsequent designation, Schumacher 1817): *Venus pennsylvanica* Chemnitz. Recent, West Indies.

* Gabb (1864) 174, 232. *pl. 24, f. 157;* as *Cardita hornii.*
† Weaver & Palmer (1922) 19. *pl. 9, f. 4, 5; pl. 10, f. 8;* as *Venericardia clarki.*
‡ Arnold & Hannibal (1914) 907; as *Venericardia aragonia.*

Lucina (?) bramkampi NEW SPECIES

PLATE 10, FIGURE 9

Lucina (?) sp. Dickerson (1916) 426 (loc. 1817).

Holotype 15629; loc. 1817; length (incomplete) 8.0 mm., altitude 8.0 mm. (The length complete would not exceed 10.0 mm.)

DESCRIPTION.—Shell small, subcircular in outline, thin; umbo central, slightly prosogyrous; anterior dorsal edge straight; posterior dorsal margin slightly convex; anterior and ventral margins broadly rounded, the posterior straight; a well-defined groove running from the umbo to the anterior dorsal margin, a less well-defined groove to the posterior end; surface with a series of step-like concentric ridges overlapping toward the beak, no incremental lines or radial ribbing visible; interior not seen.

COMPARISON.—*L. bramkampi* may be distinguished from all described West Coast lucinoid species by the overlapping, step-like character of the sculpturing.

Named in honor of Dr. Richard A. Bramkamp.

Subgenus **HERE** Gabb 1869

TYPE SPECIES (by monotypy): *Lucina* (*Here*) *richthofeni* Gabb = *Lucina excavata* Carpenter. Pliocene, California.

The species here referred to *Here* Gabb is in the adult stage similar to immature specimens of *L. excavata* in the nature of the impressed lunular area and the crenulate inner margin of the valves. Adult specimens of *L. excavata* have a much more sharply impressed lunular area and generally lack crenulate margins.

Lucina (Here) taffana (Dickerson)

PLATE 10, FIGURES 1, 2, 3, 5

Phacoides (*Myrtea*) *taffana* Dickerson (1916) 485 (described, loc. 672).
Lucina (*Myrtea*) *taffana* Dickerson (1916) 431, 445. *pl. 36, f. 11* (check list and figure).
Lucina taffana Dickerson; Clark (1926) 114 (Coalinga).
Phacoides cf. *taffana* Dickerson; M. A. Hanna (1927) 284 (La Jolla formation).

Holotype 11789; loc. 672; length 6.0 mm., altitude 5.9 mm.
Topotype 32828; loc. 672; length 5.0 mm., altitude 5.4 mm.

Dickerson, in his formal description, referred this species to *Phacoides* (*Myrtea*), but in his check-lists, and in the illustration accompanying the description, he considered it as *Lucina* (*Myrtea*).

The original description contains several errors which are apparent when the holotype is studied. The beak is strongly prosogyrate, not opisthodetic; the right valve has a single cardinal, which is not bifid.

This error was probably due to Dickerson's mistaking the edge of the lunule for a cardinal tooth, and the anterior portion of the nymph-plate for the other half of the "bifid" cardinal. The prominent, lamelliform, concentric ribs are not correctly referred to as growth-lines, as lines of growth are to be observed in the interspaces between the ribs.

Genus MILTHA H. & A. Adams 1857

GENOTYPE (by monotypy): *Lucina childreni* Gray. Recent, Brazil.

Subgenus EOMILTHA Cossmann 1910

TYPE SPECIES (by original designation): *Lucina contorta* Defrance. Eocene, Paris Basin France.

Miltha (Eomiltha ?) packi (Dickerson)

PLATE 10, FIGURES 8, 12

Dosinia gyrata Gabb (1869) 241 (Griswold's). Not *D. gyrata* Gabb (1864).
Lucina packi Dickerson (1916) 431, 445, 484. *pl. 36, f. 12* (described, loc. 672).—Clark (1926) 114 (Coalinga).—Stewart (1930) 184 ("may be *Saxolucina*").

Hypotype 15630; loc. A-1015; length 67.5 mm., altitude 66.5 mm.
Hypotype 15631; loc. A-1016; length 67.5 mm., altitude (incomplete) 61.3 mm.

The type is an immature individual; adult specimens attain a much greater size. The posterior dorsal region of the shell has two grooves: one, bounding the area, runs from the beak to the straight posterior margin; the other extends from the beak to the middle of the posterior extremity. Anterior to the beak is a small groove extending to the anterior dorsal edge.

This species is questionably referred to *Eomiltha* as it differs from *Miltha* (*sensu stricto*) only in the absence of the posterior lateral. In the type of *Eomiltha* and also in the Claiborne species *M.* (*Eomiltha*) *pandata*, the interior of the shell is rugose and roughened. In *M. packi* this is smooth as in *Miltha* (*sensu stricto*). The Miocene form *Miltha* (*Miltha*) *sanctaecrucis* (Arnold*) shows great variation in the development of this lateral and in some specimens it is entirely obsolete. It is suggested that *Miltha* (*sensu stricto*) may have originated in the California province, with *M. packi* as an ancestral type.

Genus MYRTEA Turton 1822

GENOTYPE (by monotypy): *Venus spinifera* Montagu 1803. Recent, Salcomb Bay, England.

Subgenus MYRTUCINA NEW SUBGENUS

TYPE SPECIES: *Lucina roseburgensis* Hendon. Eocene, Oregon.

* Arnold (1909) 57. *pl. 6, f. 6;* as *Phacoides sanctaecrucis.*

Venus spinifera Montagu, the type of *Myrtea*, is characterized by the presence of a single cardinal in the right valve and two cardinals in the left valve. The right cardinal is thin and directed anteriorly; below the anterior end of the lunule and the posterior end of the escutcheon are small, subobsolete laterals. The anterior cardinal in the left valve is thin, the posterior long and curved anteriorly. The laterals are not received upon the hinge-plate, but within the cavity of the shell, there being a small tubercle developed ventrally to form a socket-like depression. The lunule is unequally divided, the larger portion being in the left valve.

In *Lucina roseburgensis* Turner the right cardinal is trigonal in shape and directed posteriorly; the anterior and posterior cardinals of the left valve are of equal strength, the anterior being slightly curved, the posterior straight. The laterals are received upon the hinge-plate on a platform-like swelling. The lunule is unequally divided between the valves, the larger portion being in the right valve. Externally the shape of this species is more typically lucinoid than in *Myrtea* (*sensu stricto*), but the sculpturing consists solely of growth-lines.

The subgenus *Myrtucina* is therefore proposed for those forms with the dental formula of *Myrtea*, in which the right cardinal is trigonal in shape and the laterals are received upon the hinge-plate, but which possess a lucinoid shape.

Myrtea (Myrtucina) roseburgensis (Hendon)

PLATE 10, FIGURES 11, 13, 14, 15

Lucina roseburgensis Hendon in Turner (1938) 51. *pl. 9, f. 12, 13.*

Hypotype 15632; loc. A-1135; length 42.3 mm., altitude 39.7 mm.
Hypotype 15633; loc. A-1135; length 28.0 mm., altitude 27.0 mm.
Hypotype 15634; loc. A-1017 (incomplete).
Hypotype 15635; loc. A-1017 (incomplete).

Family UNGULINIDAE

Genus TARAS Risso 1826

GENOTYPE (by monotypy): *Taras antiquatus* Risso = ? *Tellina rotundatus* Montagu. Pliocene-Pleistocene, Trinité (Riviera).

As indicated by Stewart (1930: 193), *Diplodonta* Bronn 1831 is a subjective synonym of *Taras* Risso 1826. The genus *Zemysia* Finlay 1926, type (by original designation) *Lucina zelandica* Gray, proposed for *Diplodonta* Bronn 1831, not *Diplodon* Spix 1827, is also, therefore, a subjective synonym of *Taras*.

Taras unisulcatus NEW SPECIES

PLATE 10, FIGURES 4, 7, 10

Holotype 15636; loc. 672; length 5.8 mm., altitude 5.7 mm.
Paratype 15637; loc. 672; length 5.4 mm., altitude 5.1 mm.
Paratype 15638; loc. 672; length (incomplete) 6.8 mm., altitude 8.5 mm.

DESCRIPTION.—Shell small, thin, moderately inflated; umbos prominent, slightly anterior; posterior dorsal margin slightly convex; posterior margin straight or slightly concave, the ventral anterior and anterior dorsal margins broadly rounded; a distinct posterior groove extending from the umbo to the center of the posterior margin; surface ornamented by fine, microscopic incremental lines; nymph-plates narrow, elongate; both cardinal teeth of right valve of hinge oblique, the posterior deeply bifid; posterior cardinal of the left valve oblique, the anterior bifid, straight.

COMPARISON.—*Taras unisulcatus* may be distinguished from all other described species in the presence of the posterior groove. It is more inflated than *T. cretaceus* (Gabb*) and less so than "*Mysia*" *polita* Gabb, and may be distinguished from both species by the presence of the straight posterior margin as well as the posterior groove.

T. unisulcatus is present in the Domengine at Martinez, and a fine specimen was found among Gabb's material labelled *Mysia polita*.

Taras (?) politus (Gabb)

PLATE 10, FIGURE 6

? *Mysia polita* Gabb (1864) 178, 233. *pl. 30, f. 256* (described, Domengine, Martinez).—Gabb (1869) 244 (New Idria).
Mysia ? polita Gabb; Stanton (1896) 1027 (New Idria).
Diplodonta polita Gabb; Dickerson (1916) 430, 445 (loc. 672). Clark (1926) 114 (Coalinga).
"*Mysia ?*" *polita* Gabb; Stewart (1930) 193. *pl. 7, f. 6* (synonymy).

Holotype 11990; State Survey no. 243; length 5.9 mm., altitude 5.5 mm.

The figure given by Stewart is too poor to be identified with certainty, but appears not to be conspecific with Gabb's species, the type of which is here refigured.

Several specimens in the collections from the Domengine formation are too poorly preserved to give any additional information as to the systematic position of the species.

Family CARDIIDAE

Genus PLAGIOCARDIUM Cossmann 1886

GENOTYPE (by subsequent designation, Crosse 1886): *Cardium granulosum* Lamarck. Eocene, Lutetian-Bartonian, Paris Basin.

* Gabb (1864) 177. *pl. 30, f. 255;* as *Lucina cretacea*.

Subgenus **SCHEDOCARDIA** Stewart 1930

TYPE SPECIES (by original designation): *Cardium hatchetigbeense* Aldrich. Eocene, Wilcox, Alabama.

Plagiocardium (Schedocardia) brewerii (Gabb)

PLATE 11, FIGURES 1, 2, 3, 4

Cardium brewerii Gabb (1864) 173, 232. *pl. 24, f. 155* (described, Tejon).—Gabb (1869) 242 (Griswold's).—Cooper in Watts (1894) 57 (San Joaquin Coal Mine).—Stanton (1896) 1026 (New Idria).—Arnold (1909) 13 (Reef Ridge and northwest of Coalinga).—Arnold & Anderson (1910) 70 (Reef Ridge and northwest of Coalinga).—Clark (1926) 114 (Coalinga).

Plagiocardium (*Schedocardia*) *brewerii* (Gabb); Stewart (1930) 256 (synonymy), 257. *pl. 12, f. 6* (lectotype).

Hypotype 15639; loc. 672; length 10.0 mm., altitude (incomplete) 7.1 mm.
Hypotype 15640; loc. A-1010; length (incomplete) 15.3 mm., altitude 16.2 mm
Hypotype 15641; loc. A-1016; length 13.2 mm., altitude 13.3 mm.
Hypotype 15642; loc. A-819; length 16.0 mm., altitude 17.7 mm.

The specimens from the Domengine formation agree with those from the Tejon in the shape and the number of ribs, but no specimens in the collection attain the size exhibited by those from the type locality. The hinge is here figured for the first time; the cardinals are oblique, the anterior cardinal of the left valve is larger than the posterior, which appears as a swelling upon the valve-margin. The posterior cardinal in the right valve is slightly larger than the anterior; in the specimen figured they are fused throughout most of their length, a common character. The laterals and their adjoining sockets are well developed in the right valve. The posterior lateral and socket on the left valve are also well developed, but the anterior lateral appears only as a tubercle on the valve-margin and no socket for the reception of the right anterior lateral has been observed.

Hypotype 15641, from loc. A-1016, shows remnants of the spines which ornamented this species. They are preserved only in the interspaces, appearing as nodes on sides of the radial ribs.

Plagiocardium (Schedocardia) brewerii (Gabb) hartleyense (Clark & Woodford)

PLATE 11, FIGURE 7

Cardium brewerii "Gabb"; Dickerson (1916) 426, 427, 430, 444 (loc. 1817).
Cardium brewerii Gabb n. subsp. Clark (1921) 158 ("Meganos" north of Coalinga).
Cardium (*Pingecardium*) *hartleyensis* Clark & Woodford (1927) 94. *pl. 15, f. 11* (described, Meganos formation).

Hypotype 15643; loc. 1817; length 8.6 mm., altitude 8.8 mm.

This subspecies occurs only in the collections from locality 1817, Arroyo Hondo formation. All the specimens have 22 or 23 ribs and a less pronounced umbonal ridge than in typical *P. brewerii*, and are

much smaller in size. *P. brewerii hartleyense* was described from the Meganos formation north of Mount Diablo; it also occurs in the Santa Susana formation of the Simi Valley.

Genus TRACHYCARDIUM Mörch 1853

GENOTYPE (by subsequent designation, von Martens 1869): *Cardium isocardia* Linnaeus. Recent, West Indies.

Subgenus AGNOCARDIA Stewart 1930

TYPE SPECIES (by original designation): *Cardium (Trachycardium) claibornense* Aldrich 1911. Eocene-Claiborne, Mississippi.

Trachycardium (Agnocardia) sorrentoense (M. A. Hanna)

Cardium "*sorrentoensis*" M. A. Hanna (1927) 285. *pl. 41, f. 10, 12, 14* (described, La Jolla formation).—M. A. Hanna; Clark in M. A. Hanna (1927) 260 (Domengine, at Coalinga).

Several specimens, with flat-topped ribs separated by interspaces approximately as wide as the ribs, occur in the collection. They are not well preserved and the exact number of ribs is indeterminable, although more than 40 are present.

Genus NEMOCARDIUM Meek 1876

GENOTYPE (by monotypy): *Cardium semi-asperum* Deshayes. Eocene, Paris Basin.

Nemocardium linteum (Conrad)

PLATE 11, FIGURES 6, 9

Cardium linteum Conrad (1855) 7, 9 (*nomen nudum*); Conrad (1858) 318, 320. *pl. 2, f. 1* (described, Tejon). Not *Cardium (Protocardium) linteum* Conrad (1860) 278. *pl. 46, f. 17* (Renamed *Cymbophora intoxicata* Hanna (1924) 164).
Cardium cooperii Gabb (1864) 172, 232. *pl. 24, f. 154, a* (described, Rose Canyon, San Diego County?—lectotype from Martinez).—Turner & Stanton (1894) 95 (New Idria).—Stanton (1896) 1026 (New Idria).—Anderson (1905) 164, 166 (Avenal sandstones, coal mines, and north of Los Gatos Creek).—Anderson (1908) 13 (Salt Creek), 15 (Oil City, Domengine Ranch).—Turner in Anderson (1908) 11 (New Idria).—Arnold (1909) 13 (Reef Ridge; southwest of Domengine's Ranch), *pl. 3, f. 3* (Reef Ridge).—Arnold & Anderson (1910) 70 (Reef Ridge; southwest of Domengine's Ranch), *pl. 25, f. 3* (Reef Ridge).—Dickerson (1916) 426, 427 (loc. 1817), 430 (between Domengine and Cantua creeks), 444.—Clark (1926) 114 (Coalinga).—Clark in M. A. Hanna (1927) 260 (near Coalinga).
Cardium linteum "Gabb;" Cooper in Watts (1894) 57 (San Joaquin Coal Mine).
Cardium dalli Dickerson (1913) 264, 267, 271, 272, 273, 289. *pl. 14, f. 4, a, b, c* (described, Marysville Buttes). Not *Cardium dalli* Heilprin (1887) 131. *pl. 16a, f. 70*.
Cardium "*marysvillensis*" Dickerson (1916) 430 (between Domengine and Cantua creeks), 482 (new name for *C. dalli* Dickerson).—Clark (1921) 158 ("Meganos" north of Coalinga).
Nemocardium linteum (Conrad) Stewart (1930) 275, 276, 277 (synonymy). *pl. 8, f. 6*.—Merriam & Turner (1937) 99 (loc. 1817).

Hypotype 15644; loc. 7147; length 22.0 mm., altitude 21.6 mm.
Hypotype 15645; loc. 672; length (incomplete) 17.0 mm., altitude (incomplete) 17.5 mm.

This species is variable in outline, and a series of specimens indicates that the forms described on the basis of differences in outline must fall into synonymy with *N. linteum*. The hinge shows the very unequal cardinals characteristic of *Nemocardium*.

Family VENERIDAE

Genus MERCIMONIA Dall 1902

GENOTYPE (by original designation): *Venus bernayi* Cossmann. Eocene. Bartonian, Paris Basin.

Mercimonia bunkeri (M. A. Hanna)

PLATE 11, FIGURE 12

? *Chione varians* "Gabb"; Cooper in Watts (1894) 57 (San Joaquin Coal Mine). Not *Chione varians* Gabb (1864), a Chico species.

? *Clisocolus dubius* "Gabb"; Cooper in Watts (1894) 57 (San Joaquin Coal Mine). Not *Clisocolus dubius* Gabb (1864), a Chico species.

Dosinia sp. Anderson (1905) 166 (north of Los Gatos Creek).

Dosinia bunkeri M. A. Hanna (1927) 287 *pl. 42, f. 4, 6* (described, La Jolla formation). Stewart (1930) 229 ("may be a *Cyclinella*").

Mercimonia bunkeri (M. A. Hanna); Turner (1938) 60. *pl. 10, f. 5–9* (Oregon).

Hypotype 32962; loc. 3314; length (incomplete) 40.4 mm., altitude 41.0 mm.

Genus PACHYDESMA Conrad 1854

GENOTYPE (by monotypy): *Cytherea (Trigonella) crassatelloides* Conrad = *Donax stultorum* Mawe. Recent, California.

Pachydesma packardi (Dickerson)

PLATE 11, FIGURE 5

Tivela packardi Dickerson (1916) 432, 447, 486. *pl. 38, f. 2a, 2b* (described, loc. 672).—Clark (1926) 115 (Coalinga).—M. A. Hanna (1927) 290 (compared to *T. cliffensis*).

Topotype 15719; loc. 672; length 13.0 mm., altitude 10.0 mm.

This species was described by Dickerson from the Domengine formation at locality 672, north of Coalinga.

ADDITIONAL NOTES.—The lunule is long and narrow, defined by an impressed line; sculpture consisting of broad concentric ribs overlapping, shingle-like, toward the beaks, obsolete on the center of the valves, and more prominent on the anterior and posterior slopes and near the ventral margin. The right valve has three cardinal teeth and a distant anterior lateral socket; the nymph is large and smooth; the posterior cardinal grooved, narrow, and almost vertical; the median cardinal long, thin, in a line with the interior edge of the lateral socket; the anterior cardinal thin, near the edge of the shell, and in line with the external lamella of the lateral socket.

With the exception of a single specimen from loc. 4170 at Big Tar Canyon, all the specimens representing this species in the collections are from the type locality.

Pachydesma sulcataria NEW SPECIES

PLATE 11, FIGURES 8, 10, 14

Holotype 15648; loc. A-1022; length 19.0 mm., altitude 14.8 mm.
Paratype 15649; loc. A-816; length (incomplete) 22.0 mm., altitude 21.0 mm.
Paratype 15650; loc. A-819; length (incomplete) 18.0 mm., altitude 13.8 mm.

DESCRIPTION.—Shell thin, inflated, elongate-ovate; beaks small, central, prominent, very slightly prosogyrate; ventral margin broadly rounded; posterior margin subtruncate and straight; anterior margin sharply rounded; posterior dorsal margin straight, anterior dorsal margin concave; surface of the valve with a strong median umbonal inflation and a marked depression immediately posterior, passing from the beak to the posterior ventral margin; sculpture consisting of a few low, rounded, subobsolete concentric ridges and growth-lines; lunule lanceolate, smooth, defined by an incised line; escutcheon not defined; right valve with three cardinal teeth and a distant anterior lateral socket, the posterior cardinal heavy and trigonal, the median heavy, vertical, the anterior short, thin and near the valve margin; anterior lateral socket long, narrow; nymph smooth.

COMPARISON.—*P. sulcataria* may be distinguished from all described species by the presence of the median inflated area, with the adjacent posterior umbonal depression.

Pachydesma kelloggensis (Clark & Woodford) **mclurensis** NEW SUBSPECIES

PLATE 11, FIGURES 13, 16, 18

Holotype 15646; loc. A-818; length (incomplete) 45.6 mm., altitude 43.5 mm.
Paratype 15647; loc. A-1165; length 44.5 mm., altitude 43.4 mm.

DESCRIPTION.—Shell moderately large, heavy, trigonal; umbos central, prominent; posterior and anterior dorsal margins straight to slightly concave; anterior and posterior margins rounded, the former more sharply; ventral margin regularly and broadly rounded; lunule and escutcheon not defined; surface smooth, marked by lines of growth; hinge in right valve with three cardinals and a distant anterior lateral socket; posterior cardinal heavy, almost vertical, the median heavy, subtrigonal, the anterior thin, appressed to the shell-margin; anterior

lateral socket deep, the inner wall thick, the outer wall marked by a long thin lamellar tubercle; nymph large, heavy, rugose; left hinge not seen; pallial sinus not seen.

COMPARISON.—*P. kelloggensis mclurensis* differs from *P. kelloggensis* (Clark & Woodford*) in outline; the posterior margin is more broadly rounded than the anterior, rather than less broadly rounded and subangulate, and there is no evidence of flattening on the posterior surface of the valve. It is larger and the valve is much higher in proportion to its length than is the case in *P. weaveri* (Dickerson†).

Genus **EOMERETRIX** Turner 1938

GENOTYPE (by original designation): *Pitaria martini* Dickerson. Eocene, Oregon.

"The affinities of this genus lie with *Pachydesma*, *Meretrix*, and *Cytheriopsis*. From all of these it may be separated by the V-shaped pallial sinus, from *Meretrix* by the better-defined lunule, from *Pachydesma* and *Cytheriopsis* by the right anterior cardinal directed across the proximal end of the lateral socket as in *Meretrix* instead of closely hugging the shell margin."‡

Eomeretrix lillisi (Dickerson)

PLATE 11, FIGURES 11, 15, 17

Crassatellites lillisi Dickerson (1916) 426, 427, 430, 482. *pl. 36, f. 10* (check-lists and description, loc. 1817).—Clark (1921) 158 ("Meganos" north of Coalinga).

Topotype 15651; loc. 1817; length 14.0 mm., altitude 10.5 mm.
Topotype 15652; loc. 1817; length (incomplete) 14.2 mm., altitude 11.0 mm
Topotype 15653; loc. 1817; (incomplete).

The type, which is the largest specimen known, is badly crushed, the posterior end being lost and the lunular area so crushed as to indicate a deep, *Crassatella*-like lunule. As a result of this crushing the original figure suggests a beak which is more attenuated and prominent than is actually the case. The dimensions of the type, as given by Dickerson, are apparently based upon his conception of the dimensions of the specimen before it was crushed. The actual dimensions are: length 24.8 mm., altitude 17. 5 mm. On the basis of the topotype material at hand the following revisions may be made in the original description: beak slightly anterior; posterior dorsal margin concave near the beak, and strongly convex at the posterior end, there rounding to the broadly rounded posterior end; lunule long, bounded by an

* Clark & Woodford (1927) 98. *pl. 17, f. 7–11;* as *Tivela kelloggensis.*
† Dickerson (1914 b) 117. *pl. 11, f. 3 a, b, c;* as *Tivela weaveri.*
‡ Turner (1938) 59.

incised line; escutcheon apparently not developed; right hinge with 3 diverging cardinal teeth, the anterior cardinal long and narrow, the median cardinal short, trigonal, and directed slightly anteriorly, the posterior cardinal somewhat elongate and grooved; nymph distant from the cardinals, apparently smooth.

The only hinge which the writer was able to expose was broken anteriorly and the nature of the lateral socket was not determined. However, it is more remote from the anterior cardinal than is the case in the genotype species.

COMPARISON.—*Eomeretrix hillisi* differs from *E. martini* in shape; the posterior end is broader, the anterior more sharply rounded. The umbos are smaller and less inflated, the lunule longer in proportion to the length of the anterior dorsal margin and more sharply bounded by an incised line. The anterior cardinal is longer, and the median cardinal shorter and more trigonal.

Genus MACROCALLISTA Meek 1876

GENOTYPE (by monotypy): *Venus gigantea* Gmelin = *Macrocallista nimbosa* (Solander). Recent, North Carolina to Cuba and the Gulf Coast of the United States.

Subgenus COSTACALLISTA Palmer 1927

TYPE SPECIES (by original designation): *Callista erycina* Linnaeus. Recent, Indian Ocean and China Sea.

Section MICROCALLISTA Stewart 1930

TYPE SPECIES (by original designation): *Cytherea proxima* Deshayes. Eocene, Paris Basin.

The weight to be given various characters in the determination of generic groupings is purely a matter of personal opinion. The writer does not believe that the absence of grooving upon the left anterior cardinal is sufficient to outweigh the obvious similarities of shape, character of ribbing, and the shape of the pallial sinus, as well as the general similarities of hinge-structure which tend to link *Microcallista* to the group of *Macrocallista* (*Costacallista*).

Macrocallista (Costacallista) conradiana (Gabb)

Tapes conradiana Gabb (1864) 169, 232 (in part). *pl. 32, f. 282* (described, Tejon).—Gabb (1869) 241 (Griswold's).—Cooper in Watts (1894) 56 (San Joaquin Coal Mine).—Stanton (1896) 1027 (New Idria).

Dione conradiana Conrad (1866) 7.

Microcallista ? conradiana (Gabb); Stewart (1930) 244. *pl. 12, f. 3* (synonymy).

Macrocallista conradiana (Gabb) occurs only in the collections from the Vallecitos region, from which area it was listed by Gabb and by Stanton (*loc. cit.*).

Macrocallista (Costacallista) domenginica NEW SPECIES

PLATE 12, FIGURES 1, 2, 3, 4, 5, 6, 7, 8

? "*Meretrix horni* Gabb;" Anderson (1905) 164 (Avenal Wells), 166 (coal mines; north of Los Gatos Creek) (in part).—Anderson (1908) 15 (near Domengine Ranch).
Meretrix hornii Gabb; Dickerson (1916) 431 (in part), 445 (in part), (not *pl. 38, f. 1 a, b*) (between Domengine and Cantua creeks).
Meretrix uvasana "Conrad;" Arnold (1909) 13 (Reef Ridge and Domengine's Ranch). *pl. 3, f. 13*.—Arnold & Anderson (1910) 70 (Reef Ridge and Domengine's Ranch). *pl. 25, f. 13*.

Holotype 15654; loc. 3315; length 32.4 mm., altitude 22.3 mm.
Paratype 15655; loc. 3958; length 32.8 mm., altitude 23.2 mm.
Paratype 15656; loc. A-975; length (incomplete) 27.8 mm., altitude 20.5 mm.
Paratype 15657; loc. A-1220; length 29.6 mm., altitude 20.0 mm.
Paratype 15658; loc. 3315; length (incomplete) 31.5 mm., altitude 22.5 mm.
Paratype 15659; loc. 3315, length (incomplete) 32.3 mm., altitude 24.2 mm.

DESCRIPTION.—Shell of medium size, ovate; beak prominent, situated one third of the distance from the anterior end; ventral margin regularly rounded; anterior and posterior margins sharply rounded; posterior dorsal margin broadly convex; ventral dorsal margin straight; surface sculptured with irregularly spaced, broad, flattened concentric ribs separated by narrow, round-bottomed or V-shaped interspaces, these more sharply angulate anteriorly; lunule small, bounded by an impressed line; hinge macrocallistiform; pallial sinus not seen.

COMPARISON.—*M. domenginica* resembles *M. tecolotensis* M. A. Hanna (1927: 287. *pl. 38, f. 2, 4, 5, 6, 13*) in the nature of the concentric sculpturing, but differs from that species in shape; the umbos are larger and more prominent, the posterior end is more sharply rounded, being almost as sharply rounded as the anterior end, and the posterior dorsal margin is more convex. The ribbing also shows less of the tendency to become obsolete that is characteristic of the San Diego species. In *M. williamsoni* Weaver & Palmer (1922: 21. *pl. 10, f. 1, 11*) the umbos are more anterior and less prominent, and the concentric ribbing is prominently crested or ridged, particularly near the anterior and posterior margins. *M. domenginica capayana* is much smaller, with finer ribbing.

Macrocallista (Costacallista) domenginica capayana NEW SUBSPECIES

PLATE 12, FIGURES 9, 10

Meretrix hornii Gabb; Dickerson (1916) 426, 427, 431 (in part), 445 (in part), (not *pl. 38, f. 1a, b*). (loc. 1817.)
Macrocallista conradiana meganosensis "Clark & Woodford;" Merriam & Turner (1937) 99 (loc. 1817).

Holotype 15660; loc. 1817; length (incomplete) 18.8 mm., altitude 13.3 mm.
Paratype 15661; loc. 1817; length 18.6 mm., altitude 14.0 mm.

DESCRIPTION.—Shell similar to *M. domenginica*, but much smaller,

with more prominent, inflated umbos; the ribbing finer, more regularly spaced and with deeper, more angulate interspaces.

Genus NITIDAVENUS NEW GENUS

GENOTYPE: *Cytherea nitida* Deshayes. Eocene, Lutetien, Paris Basin.

Marcia ? conradi Dickerson and *Isocardia tejonensis* Waring, from the California Eocene, resemble *Cytherea nitidula* Lamarck and *Cytherea nitida* Deshayes (PLATE 12, FIGURE 12) from the Eocene of the Paris Basin in hinge-characters and pallial sinus.

The Paris Basin species were considered to represent *Cytherea* (*sensu stricto*) by Cossmann in 1886 (118), were referred to *Aphrodina* Conrad by Jukes-Browne (1908: 156), and were figured as "*Meretrix* (*Callocardia*)" by Cossmann & Pissarro (1904: *pl. 11, f. 50-21, 50-23*). Stewart (1930: 248, 251) indicated that they were not referable to *Aphrodina* and that there was apparently no generic name available for them.

There are 3 cardinal teeth in each valve (PLATE 12, FIGURES 17, 18), the posterior cardinal of the right valve is distant from the nymph, very wide, deeply grooved, and curved anteriorly, continuing over the median cardinal to form the long, slender, oblique anterior cardinal; the median cardinal is narrow and almost vertical. The anterior side of the posterior cardinal and the posterior side of the anterior are undercut. There is a well developed small anterior lateral socket, buttressed dorsally and ventrally by small lamellar tubercles. The left valve shows a small, elongate anterior lateral with a narrow anterior cardinal adjacent. The median cardinal is heavy, and joined dorsally to the anterior cardinal a short distance below the dorsal edge of the valve. The posterior cardinal is long, thin, appressed to the nymph-plate, but tending to curve away from it ventrally; it is strongly undercut throughout. The nymph is finely striated longitudinally.

The pallial sinus is long, ascending, and somewhat pointed at the end. The lunule is large, slightly impressed, and bounded by an incised line; escutcheon not defined. The posterior edge of the right valve is grooved to receive the beveled edge of the left.

The position of the anterior lateral tooth of the right valve appears to be the most variable feature in the development of the hinge. In *N. nitidula* (Lamarck) it is near the dorsal margin of the valve, in *N. tejonensis* (Waring) it is parallel with the nearly vertical median cardinal. *N. nitida* (Deshayes) and *N. conradi* (Dickerson) are inter-

mediate in development between these two extremes as, judging from the figures, is *N. tranquilla* (Deshayes) (Cossmann & Pissarro 1904: *pl. 11, f. 50-22*).

Nitidavenus somewhat resembles *Atopodonta* Cossmann 1886, and *Callocardia* Adams 1864, in the joining of the cardinal teeth dorsally, but differs from both in possessing a well-developed pallial sinus. *Aphrodina* possesses a rugose anterior lateral which is longer and more strongly developed than in *Nitidavenus*.

Nitidavenus conradi (Dickerson)

PLATE 12, FIGURES 19, 20, 21

Meretrix fragilis "Gabb"; Anderson in Dumble (1912) 32 (Salt Creek, N. of Coalinga). Not *Meretrix fragilis* Gabb (1869) 185, 240. *pl. 30, f. 77.*

Marcia ? conradi Dickerson (1916) 426, 427, 431 (loc. 672, in error), 445 (Concord Quad., N. and S. of Mount Diablo, in error), 484. *pl. 38, f. 3* (described, loc. 1817).—Clark (1921) 158 ("Meganos," N. of Coalinga).

Pitaria conradi (Dickerson) Clark & Woodford (1927) 95 (Meganos).

Topotype 15664; loc. 1817; length 28.8 mm., altitude 26.3 mm.
Topotype 15665; loc. 1817; length (incomplete) 25.0 mm., altitude (incomplete) 24.0 mm.

The type of this species is an immature specimen, although Dickerson's figure is slightly less than natural size rather than "× 2" as stated. Topotype 15664 represents a more fully adult specimen. The umbo is anterior, but is more than one third the distance from the anterior end; the lunule is large, slightly impressed and bounded by an incised line; the surface is sculptured by regularly spaced incised lines which appear to correspond with the lines of growth. The hinge is characteristic of the genus, although the right anterior cardinal is more nearly parallel with the median cardinal than is the case in the type species.

N. conradi occurs in the Coalinga district only at the type locality in the Arroyo Hondo formation. It is also present in the Meganos formation north of Mount Diablo.

Nitidavenus tejonensis (Waring)

PLATE 12, FIGURES 11, 13, 14, 15, 16

Isocardia tejonensis Waring (1914) 784, 785 (described, "one and one-half miles east of the McCray Wells, Ventura County").—Waring (1917) 93. *pl. 15, f. 14*

Isocardium "tejonensis" Waring; Dickerson (1916) 426, 427, 431 (loc. 1817).—Clark (1921) 158 ("Meganos" north of Coalinga).—Clark (1926) 114 (Coalinga).

Hypotype 15666; loc. 1817; length 17.0 mm., altitude (incomplete) 14.2 mm.
Hypotype 15667; loc. 1817; length (incomplete) 15.8 mm., altitude 14.3 mm.
Hypotype 15668; loc. 1817; length (incomplete) 16.9 mm., altitude 15.5 mm.
Hypotype 15669; loc. 1817; length 17.7 mm., altitude 15.7 mm.

This species is characterized by its high, inflated beaks, which are markedly prosogyrous. The hinge-plate is narrow and the hinge-elements appear to be "crowded" upon it. The anterior cardinal of the right valve is heavy and curved strongly over the median cardinal, which is proportionally smaller than is typical.

N. tejonensis is abundant in the collections from loc. 1817, but only four specimens, questionably referable to this species, occur in the Domengine collections.

Genus PITAR Rómer 1857

GENOTYPE (by monotypy): *Venus tumens* Gmelin. Recent, West coast of Africa.

Subgenus CALPITARIA Jukes-Browne 1908

TYPE SPECIES (by original designation): *Callista sulcataria* (Deshayes) = *Cytherea sulcataria* Deshayes. Eocene, Paris Basin.

Pitar (Calpitaria) campi NEW SPECIES

PLATE 13, FIGURES 1, 2, 3, 7

Holotype 15670; loc. 3315; length 48.0 mm., altitude 37.0 mm.
Paratype 15671; loc. A-975; length 44.0 mm., altitude 40.4 mm.
Paratype 15672; loc. A-975; length 37.8 mm., altitude 29.0 mm.
Paratype 15673; loc. A-1220; length (incomplete) 37.0 mm., altitude 28.9 mm.

DESCRIPTION.—Shell large, subtrigonal, moderately inflated; umbos prominent and situated approximately one fourth the distance from the anterior end; ventral and anterior margins broadly and regularly rounded; posterior margin varying from sharply rounded to subtruncate; posterior dorsal margin convex; anterior dorsal margin concave; lunule small, impressed, bounded by a poorly defined incised line; escutcheon not delimited; surface sculptured by numerous fine, close-set lamellar ribs separated by interspaces of slightly greater width (three to the one millimeter interval on the center of the shell of the holotype); hinge typical of the subgenus; pallial sinus broad, short, rounded.

COMPARISON.—*Pitar campi* differs from *P. uvasana* (Conrad*) in both shape and sculpturing; the posterior end is more produced and not rounded as in that species, the beaks are smaller and less inflated, and the lunule smaller and not so well defined. The concentric sculpturing is much finer and the ribs are closer together.

In the area studied *Pitar campi* occurs only in the apparently shallow-water deposits north of Coalinga and the basal beds of the Domengine section along Reef Ridge. It is also present at Mount Diablo.

* Conrad (1855) 9.—Conrad (1858) 320. *pl. 2, f. 3;* both as *Meretrix uvasana.*

Named in honor of Dr. C. L. Camp of the Museum of Paleontology, University of California, Berkeley.

Subgenus LAMELLICONCHA Dall 1902

TYPE SPECIES (by original designation): *Cytherea concinna* Sowerby. Recent, Magdalena Bay south to Payta, Peru.

The species here referred to the subgenus *Lamelliconcha* differ from the type of the subgenus in apparently lacking the narrow, poorly defined escutcheon, but they agree so closely in all other characters as to make their reference to any other group seem improbable.

Pitar (Lamelliconcha) joaquinensis NEW SPECIES

PLATE 13, FIGURES 9, 10, 11, 12

Meretrix hornii "Gabb"; Arnold (1909) 13. *pl. 3, f. 9* (Reef Ridge and northwest of Coalinga).—Arnold & Anderson (1910) 70. *pl. 25, f. 9* (Reef Ridge and northwest of Coalinga).

Holotype 15674; loc. A-1027; length 18.0 mm., altitude 18.2 mm.
Paratype 15675; loc. 4175; length 21.6 mm., altitude 18.2 mm.
Paratype 15676; loc. A-1027; length 20.8 mm., altitude 15.7 mm.
Paratype 15677; loc. A-1280; length (incomplete) 19.2 mm., altitude 15 3 mm.

DESCRIPTION.—Shell of medium size, subovate to trigonal in outline; umbos large, prominent, inflated, situated approximately one fifth the distance from the anterior end; ventral margin broadly rounded; anterior margin sharply rounded; posterior margin subtruncate; posterior dorsal margin varying from slightly concave to slightly convex; anterior dorsal margin short, rounded; lunule small, bounded by an impressed line; escutcheon not defined; surface sculptured by broad, flat-topped ribs (approximately .8 mm. wide on the center of the valve of the hototype), separated by narrow, incised linear interspaces, the ribbing becoming slightly crested anteriorly and the interspaces tending to be V-shaped; hinge with 3 cardinals in each valve and a left anterior lateral: the posterior right cardinal large and deeply grooved, the median and anterior cardinals small, parallel, and directed obliquely anteriorly; anterior lateral socket deep, with a narrow channel undercutting the anterior cardinal, bounded below by a lamellar tubercle; posterior cardinal of the left valve thin and closely appressed to the nymph-plate, the median cardinal trigonal and heavy, the anterior thin; pallial sinus broad and pointed, ascending to the middle of the shell.

The description of hinge-characters is based upon material from loc. A-1003, north of Mount Diablo. The species also occurs in the Llajas formation of the Simi Valley.

COMPARISON.—*Pitar joaquinensis* may be separated from all described Eocene West Coast species by the broad, flat-topped ribbing which is separated by narrow, incised linear interspaces. *P. avenalensis* has much narrower ribbing, and is longer in proportion to the height than *P. joaquinensis.*

P. joaquinensis occurs in the supposedly deeper-water marine beds of Reef Ridge and the Vallecitos as well as at loc. 672 north of Coalinga. The height-length proportions are rather variable, the extremes being illustrated.

Pitar (Lamelliconcha) avenalensis NEW SPECIES

PLATE 13, FIGURES 4, 5, 8

Holotype 15678; loc. A-1281; length 17.3 mm., altitude 12.5 mm.
Paratype 15679; loc. A-976; length 11.0 mm., altitude 8.2 mm.
Paratype 15680; loc. A-975; length 14.0 mm., altitude 10.8 mm.

DESCRIPTION.—Shell elongate-ovate, small; umbos moderately inflated, situated approximately one third the distance from the anterior end; ventral margin broadly rounded; anterior and posterior margins rounded, the former more sharply; posterior dorsal and anterior dorsal margins straight; surface with numerous broad, flat-topped, concentric ribs separated by narrow, sharply defined interspaces, the dorsal side of the ribs dropping off vertically to the interspaces, the ventral side sloping steeply; lunule moderately large, defined by a faintly incised line beyond which the concentric ribbing is absent; escutcheon not defined; hinge typical of the subgenus; pallial sinus broad, ascending, rounded.

COMPARISON.—*Pitar avenalensis* most closely resembles "*Pitaria*" *soledadensis* M. A. Hanna (1927: 288. *pl. 32, f. 8, 9*) in shape, but differs from that species in that the ribbing is flat-topped rather than crested or V-shaped, and that the interspaces in *P. avenalensis* are vertical on the dorsal side rather than V-shaped. *Antigona kelloggi* M. A. Hanna (1927: 286. *pl. 38, f. 7, 10, 11, 12*) and "*Pitaria*" *sorrentoensis* M. A. Hanna (1927: 289. *pl. 39, f. 7, 8, 10, 14*) are also similar in shape, but differ in the nature of the concentric sculpturing.

Pitar (Lamelliconcha) hornii (Gabb) NEW SUBSPECIES

PLATE 13, FIGURE 6

Meretrix hornii "Gabb"; Dickerson (1916) 431, 445. *pl. 38, f. 1a, b* (between Domengine and Cantua creeks).

Figured specimen 15878; loc. 672; length 7.9 mm., altitude 4.6 mm.

Immature and poorly preserved adult specimens of a *Pitar* with

ribbing similar to that of *Pitar hornii* (Gabb*) from the Tejon formation occur in the collections from loc. 672 and from the Reef Ridge section. They appear to differ from typical *P. hornii* in being more broadly rounded posteriorly and less sharply rounded anteriorly, and are higher in proportion to the length of the shell. They also seem to be more inflated, but this condition may be due to the poor preservation of the adult specimens. On the immature specimens the ribbing is somewhat more strongly developed and closer together than on the Tejon material.

Stewart (1930: 242. *pl. 12, f. 8; pl. 17, f. 7*), although he had a well-preserved hinge of the Tejon form in which the anterior lateral socket was well channeled and undercut the anterior cardinal strongly, considered this species to be a *Macrocallista* (*Costacallista* ?). The external shape of the Tejon specimens is more elongate than is characteristic of *Pitar*, but the nature of the hinge, as well as the rounded pallial sinus, are indicative of *Pitar*. The Coalinga specimens are more typical in outline than the Tejon forms.

Pitar (Lamelliconcha) SPECIES

Several poorly preserved specimens of an undetermined species of *Pitar* (*Lamelliconcha*) occur in the collections from localities 4178 and A-978, in the upper zone of the Arroyo Hondo formation near Domengine Creek.

Genus PELECYORA Dall 1902

GENOTYPE (by original designation): *Cytherea hatchetigbeensis* Aldrich. Eocene, Wilcox, Alabama.

Pelecyora aequilateralis (Gabb)

PLATE 14, FIGURES 4, 6, 7, 8, 11

Venus aequilateralis Gabb (1869) 184, 239. *pl. 30, f. 76* (described, San Diego).
Pitaria aequilateralis (Gabb); M. A. Hanna (1927) 288. *pl. 39, f. 1, 2, 3, 4, 5, 9, 12* (San Diego).
Pelecyora aequilateralis (Gabb); Stewart (1930) 237, 238 (synonymy). *pl. 8, f. 13* (lectotype).

Hypotype 15686; loc. A-1020; length 20.0 mm., altitude 15.7 mm.
Hypotype 15687; loc. A-1020; length (slightly crushed) 21.6 mm., altitude 16.8 mm.
Hypotype 15688; loc. A-1020; length 18.4 mm., altitude 15.6 mm.
Hypotype 15689; loc. A-1020; (incomplete).

This species occurs only in the collections from the Vallecitos. The characteristic variations in shape and strength of the concentric sculpturing, as figured by Hanna, are all to be noted in the Vallecitos material. However, the finer ribbing appears to be more predominantly represented in our material than in that from San Diego.

* Gabb (1864) 164, 231. *pl. 23, f. 144*; as *Meretrix hornii*.

Pelecyora gabbi (Arnold)

PLATE 14, FIGURES 1, 2, 3, 5, 9

Meretrix gabbi Arnold (1909) 13, 49. *pl. 3, f. 4* (described).—Arnold & Anderson (1910) 70 *pl. 25, f. 4* (northwest of Coalinga).—Dickerson (1916) 446 (Coalinga District)

Topotype 15698; loc. 7155; length 21.8 mm., altitude 18.2 mm.
Topotype 15699; loc. 7155; length (incomplete) 21.3 mm., altitude 17.6 mm.
Topotype 15700; loc. 7155; length (incomplete) 17.7 mm., altitude 14.6 mm.
Topotype 15701; loc. 7155; (incomplete)
Topotype 15702; loc. 7155; (incomplete).

Pelecyora gabbi differs from *P. aequilateralis* (Gabb) in being more inflated and in the more rounded posterior extremity. In general it is less variable in shape and strength of sculpturing than Gabb's species.

The lunule, faintly marked, is large, as is characteristic of the genus, the pallial sinus deep, rounded, ascending. Right valve with 3 cardinal teeth and a deep anterior lateral socket; anterior cardinal small, close to the socket and strongly undercut; median cardinal trigonal and heavy; posterior cardinal elongate, grooved; nymph distant from the laterals and smooth. Left valve with 3 cardinals and an anterior lateral; anterior cardinal thin, and close to the lateral (broken in figured specimen); median cardinal short, trigonal, heavy; posterior thin and almost completely fused to the nymph; lateral small, trigonal.

Pelecyora gabbi is known in the Coalinga district only from the carbonaceous strata in the vicinity of the San Joaquin and California coal mines. It appears that some ecologic factor, perhaps indicated by the abundant carbonaceous material, explains the presence of this species here, and its absence in the Vallecitos area, where it is replaced by *P. aequilateralis*.

Genus TIVELINA Cossmann 1886

GENOTYPE (by subsequent designation, Crosse 1886): *Cytherea rustica* Deshayes. Eocene, Paris Basin.

Dall (1902: 354) designated as the type of *Tivelina* Cossmann 1886, *Cytherea tellinaria* Lamarck, the first species of Cossmann, and has been followed by Jukes-Browne and subsequent writers. All apparently have overlooked Crosse's designation* of *Cytherea rustica* Deshayes, Cossmann's second species.

Tivelina idriaensis NEW SPECIES

PLATE 13, FIGURES 13, 14, 15, 17

Holotype 15681; loc. A-1017; length 18.5 mm., altitude 12.2 mm.
Paratype 15682; loc. A-1017; length 15.5 mm., altitude 11.6 mm.

* Crosse (1886) 331.

DESCRIPTION.—Shell small, elongate; umbos inflated, high, prominent, situated at the anterior third of the shell; anterior dorsal margin convex; anterior and ventral margins rounded; posterior margin short, almost straight; posterior dorsal margin straight anteriorly, convex posteriorly; lunule large, poorly defined, bounded by a faint, impressed line; escutcheon not defined; surface sculptured by strong concentric ribbing, overlapping toward the beaks, a strong inflation extending from the posterior side of the umbos to the posterior margin; right valve of hinge with 3 cardinals and a well-developed anterior lateral socket, the anterior cardinal small, subtrigonal, undercut ventrally, the median cardinal trigonal, almost vertical, the posterior cardinal long, thin, closely appressed to the nymph-plate, the posterior cardinal margin of the shell faintly grooved; left valve with 3 cardinals and an anterior lateral, the anterior cardinal thin, almost vertical, the median cardinal trigonal, heavy, the posterior cardinal long, thin, almost completely fused to the nymph-plate; pallial sinus not seen.

COMPARISON.—*Tivelina idriaensis* differs from *T. vaderensis* (Dickerson*) in the much higher, more inflated umbos and the more sharply rounded anterior and posterior margins.

Tivelina (?) delicatina NEW SPECIES

PLATE 13, FIGURES 16, 18

Holotype 15683; loc. A-1108; length 3.5 mm., altitude 2.7 mm.
Paratype 15684; loc. A-1108; length 2.0 mm., altitude 1.8 mm. (not figured)
Paratype 15685; loc. A-1108; length 2.4 mm., altitude 1.9 mm.

DESCRIPTION.—Shell small, polished; umbos small, situated at the anterior third of the shell; anterior dorsal margin long, straight, the anterior margin short, rounded, the ventral margin broadly and regularly rounded, the posterior margin short, rounded; posterior dorsal margin long and convex; lunule long, moderately broad, defined by an impressed line; escutcheon not defined; surface ornamented by irregularly spaced incised lines, these obsolete on the center of the shell, but moderately well-developed toward the anterior and posterior dorsal margins and near the ventral edge of the shell; hinge small; 3 cardinals in the right and left valves, with an anterior lateral in the left and a corresponding socket in the right valve, the lateral being somewhat oblique; pallial sinus short.

COMPARISON.—This species is the smallest of the Eocene *Veneridae* which has as yet been recognized on the West Coast. It differs from

* Dickerson (1915) 54. *pl. 3, f. 5a, b, c;* as *Macrocallista vaderensis.*

T. idriaensis in being much less inflated, with proportionally smaller beaks. *T. vaderensis* has a relatively shorter anterior dorsal margin, a less sharply rounded anterior end, and a less convex posterior dorsal margin.

Family TELLINIDAE

Genus TELLINA Linnaeus 1758

GENOTYPE (by subsequent designation, Children 1823): *Tellina radiata* Linnaeus. Recent, West Indies

The subgeneric and sectional groups of the genus *Tellina* are based upon the hinge-characters and the condition of the pallial sinus. The type of preservation and the nature of the matrix in which the Eocene species are preserved makes the determination of the finer groupings impracticable, and there is little doubt that many forms referred to this genus will later be found to be referable to some other generic type.

Tellina soledadensis M. A. Hanna

PLATE 14, FIGURE 13

Tellina remondii "Gabb"; Stanton (1896) 1027 (New Idria).—Dickerson (1916) 431, 447 (loc. 672).
Tellina soledadensis M. A. Hanna (1927) 291. *pl. 42, f. 1, 2, 5* (described, La Jolla formation).—Clark in M. A. Hanna (1927) 260 (Domengine near Coalinga).

Hypotype 30664; loc. 672; length 44.5 mm., altitude 30.0 mm.

In his original description of this species Hanna states that "there is apparently no prominent ridge from the beak to the posterior." The Coalinga material shows that such a ridge is present, and is faintly marked by a narrow groove from the umbo to the posterior ventral margin.

Tellina joaquinensis Arnold

PLATE 14, FIGURES 15, 19, 20

Tellina hoffmaniana "Gabb"; Cooper in Watts (1894) 57 (San Joaquin Coal Mine).
Tellina joaquinensis Arnold (1909) 13, 49. *pl. 2, f. 11* (described, San Joaquin Coal Mine).—Arnold & Anderson (1910) 70. *pl. 24, f. 11* (San Joaquin Coal Mine).—Clark (1926) 115 (Coalinga).—Clark & Woodford (1927) 99 (described from Coalinga).

Topotype 15690; loc. 7155; length 22.0 mm., altitude 16.0 mm.
Topotype 15691; loc. 7155; length (incomplete) 14.2 mm., altitude 10.1 mm.
Topotype 15692; loc. 7177; length 11.2 mm., altitude 7.4 mm.

This form occurs only in the collections from the San Joaquin Coal Mine. Gabb's record (1869: 182, 237) of *Tellina hoffmaniana* from Griswold's may be based upon this species, although it does not occur in our collections from that locality.

Tellina domenginensis NEW SPECIES

PLATE 14, FIGURES 12, 14, 16, 18

Holotype 15694; loc. 3315; length 33.3 mm., altitude 20.0 mm.
Paratype 15695; loc. A-975; length (incomplete) 26.5 mm., altitude 15.7 mm.
Paratype 15696; loc. A-975; length (incomplete) 31.3 mm., altitude 22.1 mm.
Paratype 15697; loc. A-1220; length (incomplete) 34.5 mm., altitude (incomplete) 21.6 mm.

DESCRIPTION.—Shell elongate-ovate, thin; umbos small, central; anterior dorsal margin straight to slightly convex, the anterior margin broadly rounded, subtruncate, the ventral margin regularly rounded, the posterior margin sharply rounded, subangulate; posterior dorsal margin straight; umbonal angle 145 degrees; surface-ornamentation consisting only of coarse concentric lines of growth.

COMPARISON.—*Tellina domenginensis* occurs most abundantly in the coarse sandstones at the base of the Domengine formation as exposed between Oil City and Domengine Creek. It most nearly resembles *T. jollaensis* Dickerson (1916: 378, 386, 438, 447, 487. *pl. 37, f. 3*), from which it may be distinguished by its central umbos and its greater umbonal angle (135 degrees in the San Diego species), and in its less pointed posterior margin.

Tellina cf. longa Gabb

Cf. *Tellina longa* Gabb (1864) 155, 230. *pl. 22, f. 131* (described).

Several poorly preserved specimens of a *Tellina* with a concave posterior dorsal margin, somewhat rostrate, and a sculpture consisting of microscopic incremental lines, occur in the collections from the Reef Ridge and the Vallecitos regions.

Tellina SPECIES

PLATE 14, FIGURE 10

Tellina cf. *longa* Gabb; Dickerson (1916) 431 (loc. 672).

Figured specimen 15693; loc. 672; length 15.0 mm., altitude 7.1 mm

Two casts of a *Tellina*-like form occur in the collections from loc. 672. The beaks are anterior, the anterior and posterior dorsal margins straight, the ventral broadly rounded, the anterior margin straight, the posterior sharply rounded.

Genus MACOMA Leach in Ross 1819

GENOTYPE (by monotypy): *Macoma tenera* Leach = *Tellina calcarea* Gmelin. Recent, northern seas of Europe and North America.

Macoma sheridani NEW SPECIES

PLATE 14, FIGURES 21, 22

Holotype 15703; loc. A-1154; length 18.4 mm., altitude 13.2 mm.
Paratype 15704; loc. A-1154; length (incomplete) 15.5 mm., altitude 11.3 mm.

DESCRIPTION.—Shell small, thin, moderately inflated, subovate; umbos small, posterior; anterior dorsal margin slightly convex, the anterior margin broadly rounded, the ventral margin convex, the posterior margin sharply rounded; posterior dorsal margin straight; umbonal angle 138 degrees; posterior curved to right; both valves with a slight umbonal ridge to the posterior ventral edge, bordered on either side by a broad shallow fold; surface sculptured only by fine, regular, concentric lines of growth.

COMPARISON.—*Macoma sheridani* differs from *M. rosa* M. A. Hanna (1927: 292. *pl. 41, f. 2, 3, 4, 5, 8*) in lacking a sculpture of concentric ridges, in having a shorter posterior dorsal slope and a less sharply rounded posterior end, and in lacking a posterior ventral lobation. *M. viticola* Anderson & Hanna (1925: 157. *pl. 2, f. 12*) is smaller and differs greatly in outline.

Named in honor of Mr. Sheridan A. Berthiaume, graduate student at Cornell University, who collected the type specimen.

Family GARIIDAE

Genus GARI Schumacher 1817

GENOTYPE (by tautonomy); *Gari vulgaris* Schumacher = *Tellina gari* Linnaeus; Spengler & Chemnitz (*nomen dubium*). Recent, Indo-Pacific.

Gari columbiana (Weaver & Palmer)

PLATE 15, FIGURE 2

Tellina hornii Gabb ?; Stanton (1896) 1027 (New Idria).
Tellina horni Gabb; Anderson (1908) 15 (Domengine's Ranch).
? *Tellina hornii* Gabb; Arnold (1909) 13. *pl. 2, f. 9* (Reef Ridge).—Arnold & Anderson (1910) 70. *pl. 24, f. 9* (Reef Ridge).
Psammobia hornii (Gabb); Dickerson (1916) 431, 446 (in part) (loc. 672).—Clark (1926) 115 (Coalinga).
Gari hornii (Gabb); Stewart (1930) 282 (in part) (synonymy).
Psammobia columbiana Weaver & Palmer (1922) 22. *pl. 10, f. 18* (described, Coal Creek, Washington).

Hypotype 15705; loc. A-1027; length 30.0 mm., altitude 16.1 mm.

As seen by the synonymy given above, this species has been mistaken for *Gari hornii* (Gabb*). It may be distinguished from that form in having the anterior dorsal margin almost parallel to the

* Gabb (1864) 160, 161, 231. *pl. 30, f. 244;* as *Tellina hornii.*

ventral, the umbos higher and more prominent, and the shell thinner and less inflated.

Gari texta Gabb

PLATE 15, FIGURE 1

? *Gari texta* Gabb (1864) 155, 230. *pl. 22, f. 180* (described "Tejon Group, Martinez").
Gari texta (?) Gabb; Anderson (1905) 166 (north of Los Gatos Creek).
Psammobia texta (Gabb); Dickerson (1916) 431, 446 (loc. 672).
Psammobia (*Gari*) *texta* Gabb; Clark (1926) 115 (Coalinga).
"*Gari*" *texta* Gabb; Stewart (1930) 283. *pl. 7, f. 12* (holotype and synonymy).

Hypotype 33352; loc. 7004 (Simi Valley); length (incomplete) 56.8 mm., altitude 27.0 mm.

The strength of the radial ribbing varies considerably. On one specimen in the collection from loc. 672 they are dominant over the concentric ribbing. According to Stewart (1930: 283) the concentric lines are dominant on the holotype, the radials more prominent in the interspaces. On other specimens in the Domengine collections the radials are almost entirely obsolete. This species is known only from the Domengine horizon.

Gari hornii (Gabb) umpquaensis Turner

PLATE 14, FIGURE 17

Gari hornii umpquaensis Turner (1938) 62. *pl 7, f. 11.*

Holotype 33149; loc. A-662; length 38.5 mm., altitude 23.5 mm.
Paratype 33150; loc. A-662; length 30.2 mm., altitude 17.4 mm. (not figured).

Distinguished from *Psammobia columbiana* Weaver & Palmer and from *G. hornii* (Gabb) by its greater inflation and higher beak with concave profile on either side.

Several poorly preserved specimens from loc. 1817 are similar in outline but do not appear to be as greatly inflated as the Oregon specimens.

Gari eoundulata NEW SPECIES

PLATE 14, FIGURES 23, 24

Holotype 15707; loc. A-820; length 31.8 mm., altitude 16.0 mm.
Paratype 15708; loc. A-976; length (incomplete) 14.8 mm., altitude 12.0 mm.

DESCRIPTION.—Shell elongate-ovate; umbos broad, prominent, anterior; anterior dorsal margin convex, the anterior margin rounded, subtruncate, the ventral margin broadly and regularly rounded, the posterior margin truncate, straight, angulate medially; posterior dorsal margin straight; a broad umbonal groove extending to the ventral half of the posterior margin, bounded above by a well defined umbonal ridge to the posterior median angulation; a less well defined umbonal ridge extending to the middle of the anterior margin; surface

marked by numerous irregular concentric undulations, most prominently developed on the ventral edge of the posterior groove, subobsolete in the posterior groove and on the posterior and anterior ridges.

COMPARISON.—This unique little species may be distinguished from all described West American *Gariidae* by the presence of the broad posterior umbonal groove and the well-developed ridge dorsal to it, as well as by the concentric undulations over the center of the valve.

Family DONACIDAE

Genus DONAX Linnaeus 1758

GENOTYPE (by subsequent designation, Schumacher 1817): *Donax rugosa* Linnaeus. Recent, West Indies.

Donax lata Gabb

Donax "*latus*" Gabb (1869) 183, 238. *pl. 30, f. 75* (described, ten miles west of Griswold's).—Dickerson (1916) 445 (ten miles west of Griswold's, etc.)—M. A. Hanna (1927) 298 (compared to *D. scrippsensis* M. A. Hanna).—Stewart (1930) 205. *pl. 8, f. 5* (holotype).
Donax lata Stanton (1893) 110 ("oldest previously described species").
? *Donax scrippsensis* M. A. Hanna (1927) 293. *pl. 40, f. 1, 12* (described, La Jolla formation).

Donax lata is apparently based upon a single specimen, the holotype, as the species is not represented in Gabb's collections from that locality in the University of California and the writer has not succeeded in securing a specimen from the type locality of the species.

Donax scrippsensis M. A. Hanna is a smooth-shelled species when well preserved, but when weathered has radial ribbing very similar to that described by Gabb. Judging from both Gabb's and Stewart's inadequate figures of the holotype it is very probable that the ribbing may be due to weathering on that specimen also, and that in consideration of their apparent similarity of shape *D. scrippsensis* may be synonymous with *D. lata*. However, until well preserved topotype specimens of Gabb's species are found it is judged best merely to indicate the probable synonymy.

Family SOLENIDAE

Genus SOLEN Linnaeus 1758

GENOTYPE (by subsequent designation, Schumacher 1817): *Solen vagina* Linnaeus = *S. brevis* Gray. Recent, East Indies?

Solen parallelus Gabb

PLATE 15, FIGURES 6, 7

Solen parallelus Gabb (1864) 146. *pl. 22, f. 117* (described, ? Domengine, Martinez).—Stanton (1896) 1027 (New Idria).—Anderson (1905) 164 (Avenal sandstones).—Arnold (1909) 13 (N. of McLure Valley, S. W. of Domengine's Ranch).—Arnold & Anderson (1910) 70

(N. of McLure Valley and S. W. of Domengine's Ranch).—Dickerson (1916) 431 (in part) (loc. 672).

Hypotype 15709; loc. A-1009; length 27.5 mm., altitude 8.0 mm.
Hypotype 15710; loc. 672; length (incomplete) 32.0 mm., altitude 15 5 mm.

The specimens figured show a slight anterior constriction that might be considered to represent a very broad umbonal furrow differing greatly from that characteristic of *Solena* (*Eosolen*), which is narrower, deeper, and more sharply delimited.

This species is rare in the Coalinga region, and it is undoubtedly true that some of the references listed above represent incorrect determinations, probably of *Solena* (*Eosolen*) *coosensis*.

Solen (?) domenginicus NEW SPECIES

PLATE 15, FIGURES 3, 4

Holotype 15711; loc. A-1167; length (incomplete) 84.0 mm., altitude 22.5 mm.

DESCRIPTION.—Shell straight, rather heavy; anterior end sharply truncated with a narrow, shallow groove parallel with and close to the anterior end; growth-lines indicating a broadly rounded posterior end; dorsal margin posterior to the hinge, and ligamental area flaring out to form a flange-like projection which rounds posteriorly to the posterior end of the valve; ligamental area extending from the extremely anteriorly placed cardinal tooth to the beginning of the flange; surface smooth.

COMPARISON.—This species may be distinguished by the presence of the posterior dorsal flange-like projection which appears to be unique among the *Solenidae*. This is the largest *Solen* described from the West Coast Eocene deposits. The growth-lines suggest that when complete the specimen was probably 100 millimeters in length.

Genus SOLENA March 1853

GENOTYPE (by subsequent designation, Stoliczka 1871): *Solen obliquus* Spengler = *S. ambiguus* Lamarck. Recent, Caribbean Sea.

Subgenus EOSOLEN Stewart 1930

TYPE SPECIES (by original designation): *Solena plagiaulax* (Cossmann) = *Solen obliquus* Sowerby 1844, not Spengler 1794. Eocene, Paris Basin, France.

The subgenus *Eosolen* is distinguished by the presence of a distinct anterior umbonal furrow, and in being produced anteriorly. It is represented in both the Eocene and the Oligocene of the western American Tertiary, as "*Solen*" *eugenensis* Clark (1925: 98. *pl. 22, f. 1*) from the Lincoln horizon, Oligocene, of the State of Washington, and

"Solen" lorenzanus Wagner & Schilling from the San Emigdio Oligocene of California belong to this subgenus. Elsewhere apparently it is confined to the Eocene (*fide* Stewart).

Solena (Eosolen) coosensis Turner

PLATE 15, FIGURE 5

Solen novacula "Anderson & Hanna"; M. A. Hanna (1927) 294. *pl. 43, f. 1.*
Solen parallelus Gabb, Dickerson (1916) 431 (in part) (between Domengine and Cantua creeks).
Solena (Eosolen) coosensis Turner (1938) 62. *pl. 9, f. 12.*

Hypotype 15712; loc. A-1280; length (incomplete) 42.4 mm., altitude 16.8 mm.

DESCRIPTION.—Shell thin, elongate, gaping at both ends, ornamented by growth-lines and fine diagonal lines converging ventrally between the posterior furrow and the locus of the anterior ventral angle; dorsal and ventral margins practically parallel; dorsal margin slightly concave immediately in advance of the beaks; posterior area separated from the remainder of the shell by a conspicuous umbonal furrow; a slight ridge usually present immediately posterior to the furrow and fine radial lines occasionally seen on the posterior area which is semicircular in outline.

Solena (Eosolen) coosensis is distinguished from *S. columbiana* (Weaver & Palmer*) and *Solen novacularis* Anderson & Hanna by the larger, rounded posterior area.

Solena (Eosolen) subverticala NEW SPECIES

PLATE 15, FIGURE 8

Holotype 15713; loc. A-816; length (incomplete) 21.6 mm., altitude 8.6 mm.

DESCRIPTION.—Shell small, thin, elongate, gaping, ornamented by lines of growth; dorsal and ventral margins parallel, the dorsal slightly concave immediately behind the beaks; anterior end produced, rounded, separated from the rest of the shell by a conspicuous umbonal furrow set at an angle of 105 degrees to the dorsal margin; anterior side of the furrow bounded by a low ridge, and anterior to this a second shallow groove.

COMPARISON.—*S. subverticala* may be distinguished from *S. coosensis* Turner, *S. novacularis* (Anderson & Hanna†) and *S. columbiana* (Weaver & Palmer) by its smaller size, more rounded anterior end, and more vertical umbonal groove which, in these species, is set at

* Weaver & Palmer (1922) 24. *pl. 10, f. 3; as Solen columbianus.*
† Anderson & Hanna (1928) 65; as *Solen novacularis.*

angles ranging from 122 to 132 degrees to the dorsal margin of the valve. *S. stantoni* (Weaver*) resembles this species in size, but the valve is curved dorsally. The specimens figured by Clark & Woodford (1927: 103. *pl. 18, f. 9, 10*) as *S. stantoni* appear to be closely related to *S. subverticala*.

Solena (Eosolen) SPECIES

Poorly preserved specimens of a *Solena* appear to differ from described species in having a hinge that is not completely anterior, the dorsal edge of the valve being prolonged beyond the beak for a short distance. An oblique furrow is present from the hinge region to the anterior ventral margin. The anterior end is rounded from the dorsal prolongation to the ventral edge.

Family MACTRIDAE

Genus SPISULA Gray 1837

GENOTYPE (by subsequent designation, Gray 1847): *Cardium solidum* Linnaeus. Recent, European Seas.

Spisula merriami Packard

PLATE 15, FIGURES 12, 13

? *Mactra* sp. Turner & Stanton (1894) 95 (New Idria).—Stanton (1896) 1027 (New Idria).—Anderson (1905) 166 (coal mines).

Spisula merriami Packard (1916) 294. *pl. 27, f. 3, 4*.—Dickerson (1916) 431, 447, 485. *pl. 39, f. 2 a, b, c* (not *f. 2 d*) (between Domengine and Cantua Creeks).—Anderson & Hanna (1925) 150 (described from Coalinga region, Tejon record based upon *S. bisculpturata* Anderson & Hanna).—Clark (1926) 115 (Coalinga).

Spisula cf. *bisculpturata* Anderson & Hanna, Clark in M. A. Hanna (1927) 260 (Coalinga, Domengine)

Hypotype 15717; loc. A-816; length 19.6 mm., altitude 16.0 mm.
Hypotype 15718; loc. A-1008; length 29.6 mm., altitude 23.2 mm.

Additional topotype specimens of *S. merriami* show that not all the individuals develop prominent concentric ribbing over the entire surface of the shell and many exhibit a sculpturing almost exactly similar to that of *S. bisculpturata* Anderson & Hanna (1925: 149. *pl. 3, f. 7*). *S. merriami* appears to differ from that species in being more equilateral and in lacking or possessing a less prominent depression behind the anterior umbonal ridge.

Spisula capayana NEW SPECIES

PLATE 15, FIGURES 9, 10, 11

Spisula (?) sp. Dickerson (1916) 426, 431 (loc. 1817).

Syntype 15714; loc. 1817; length (incomplete) 12.8 mm., altitude (incomplete) 10.5 mm.
Syntype 15715; loc. 1817; length (incomplete) 13.3 mm., altitude 10.5 mm.
Paratype 15716; loc. 1817; length 22.7 mm., altitude 17.6 mm.

---

* Weaver (1905) 116. *pl 12, f. 1*; as *Solen stantoni*.

DESCRIPTION.—Shell small, ovate, produced anteriorly; umbos posterior to median line, inflated; anterior dorsal margin convex; anterior margin rounded, the ventral margin broadly and regularly rounded, the posterior ventral margin angulate; posterior dorsal margin broadly convex; a sharp, almost straight posterior umbonal ridge extending to the posterior ventral margin, and a poorly developed anterior umbonal ridge extending in a curve to the anterior end; center of the valve smooth except for lines of growth, the anterior and posterior dorsal slopes with prominent concentric ribbing extending to but not crossing the umbonal grooves, the ribs being finer and more numerous upon the anterior dorsal slope than upon the posterior; hinge not seen.

COMPARISON.—*S. capayana* may be distinguished from *S. bisculpturata* Anderson & Hanna (1925: 149. *pl. 3, f. 7*), which it most closely resembles, in having more inflated and prominent umbos, a more rounded anterior margin, and more convex anterior and posterior dorsal margins, giving the shell a more ovate appearance, in lacking the shallow depression immediately following the anterior umbonal ridge, and in the absence of the bisculptate condition of the sculpturing upon the anterior dorsal slope. The new species is less equilateral than *S. merriami* Packard, more broadly rounded anteriorly, the posterior umbonal ridge is more sharply developed, and the concentric sculpturing is never present upon the center of the valve. This species is known only from locality 1817.

Family CORBULIDAE

Genus CORBULA Bruguière 1797

GENOTYPE (by subsequent designation, Schmidt 1818): *Corbula sulcata* Lamarck. Recent, coast of Senegal.

Subgenus CARYOCORBULA Gardner 1926

TYPE SPECIES (by original designation): *Corbula alabamiensis* Lea. Eocene, Claiborne, Gulf Coast.

Corbula (Caryocorbula) dickersoni Weaver & Palmer

PLATE 16, FIGURES 1, 5, 9

Corbula hornii "Gabb"; Stanton (1896) 1027 (New Idria).—Dickerson (1916) 430, 444 (loc. 672).

Corbula dickersoni Weaver & Palmer (1922) 24. *pl. 9, f. 9, 10* (described. Cowlitz formation, Washington).

Hypotype 15720; loc. A-819; length 12.2 mm., altitude 7.2 mm.
Hypotype 15721; loc. A-819; length 13.6 mm., altitude 8.3 mm.
Hypotype 15722; loc. 672; length 8.9 mm., altitude 5.7 mm.

Corbula (Caryocorbula) parilis Gabb

PLATE 16, FIGURES 2, 3, 6, 7, 10

Corbula parilis Gabb (1864) 150, 229. *pl. 29, f. 239, a* (described, "Martinez, Marsh's, Cochran's, San Diego").—Gabb (1869) 234 (Griswold's).—Arnold (1909) 13 (Reef Ridge, and Domengine's Ranch) (not "San Joaquin Coal Mine," nor *pl. 2, f. 2* = *Corbula domenginica* n. sp. below).—Arnold & Anderson (1910) 70 (Reef Ridge and Domengine's Ranch), (not "San Joaquin Coal Mine" nor *pl. 24, f. 2.* = *Corbula domenginica* n. sp. below).—Dickerson (1916) 426, 427, 430, 444 (in part) (between Domengine and Cantua creeks).—Clark in M. A. Hanna (1927) 260 (Coalinga).—Stewart (1930) 288, 289 (lectotype and synonymy) (not *pl. 6, f. 3*).—Merriam & Turner (1937) 99 (loc. 1817).

Corbula "paralis Gabb"; Anderson (1905) 164 (Avenal sandstones).—Anderson in Dumble (1912) 32 (Salt Creek).

Corbula "parallelus Gabb"; Clark (1926) 114 (Coalinga).

Hypotype 15723; loc. 1817; length 9.4 mm., altitude 7.0 mm.
Hypotype 15724; loc. 1817; length 8.4 mm., altitude 7.0 mm.
Hypotype 15725; loc. 1817; length 7.1 mm., altitude 5.6 mm.
Hypotype 15726; loc. 1817; length 8.2 mm., altitude 5.5 mm.
Hypotype 15727; loc. A-976; length 9.2 mm., altitude 6.2 mm.

Stewart (1930: 288, 289. *pl. 3, f. 5*), believing that Gabb's original figure of this species was a synthetograph, designated as lectotype a specimen which is incompletely preserved. He states "the fine radiating lines of the original description are not present on this species, and evidently Gabb included more than one species in his description." Recently a specimen identified in Gabb's own handwriting has been found in the collections of the University of California (no. 33151). It is well preserved and conforms so closely to the size markings of the original figure as to be almost certainly the specimen upon which Gabb's figure was based. This specimen has well developed radial striations.

Corbula (Caryocorbula) tomulata M. A. Hanna

PLATE 16, FIGURE 11

Corbula parilis "Gabb"; Dickerson (1916) 430, 444 (in part) (between Domengine and Cantua creeks).

Corbula tomulata M. A. Hanna (1927) 297. *pl. 44, f. 1, 2, 3, 4, 5, 11, 14* (described, La Jolla formation).

Hypotype 15728; loc. A-977; length 10.0 mm., altitude 6.6 mm.

Subgenus VARICORBULA Grant & Gale 1931

TYPE SPECIES (by original designation): *Corbula gibba* (Olivi). Recent, Mediterranean Sea and west coast of Europe.

Corbula (Varicorbula) capayana NEW SPECIES

PLATE 16, FIGURES 13, 14, 15

Holotype 15733; loc. 1817; length 3.0 mm., altitude 2.6 mm.
Paratype 15734; loc. 1817; length (slightly crushed) 2.3 mm., altitude 2.3 mm.
Paratype 15735; loc. 1817; length 3.4 mm., altitude 2.7 mm.

DESCRIPTION.—Shell very small, ventricose; umbos large, inflated, prominent, high, anterior to the median line; anterior margin regularly rounded, the ventral margin broadly rounded with a tendency to be slightly concave anteriorly, the posterior margin strongly rostrate, almost straight; a strong, broad umbonal ridge extending to the posterior ventral margin with a broad, low groove immediately anterior; surface with numerous irregular concentric ribs which do not cross the umbonal ridge, the posterior marked by strong lines of growth; interior not seen.

COMPARISON.—*C. capayana* resembles *C. cliffensis* M. A. Hanna in size, but differs from that species in having much larger, more inflated umbos, and a well-developed posterior umbonal ridge delimiting a more produced posterior area. It may be distinguished from other described species by its shape and the character of the sculpturing. Known only from locality 1817, in the Arroyo Hondo formation.

Corbula (Varicorbula ?) cliffensis M. A. Hanna

Corbula cliffensis M. A. Hanna (1927) 294. *pl. 43, f. 2–5* (described, La Jolla formation).

Corbula rosecanyonensis M. A. Hanna

PLATE 16, FIGURE 17

Corbula rosecanyonensis M. A. Hanna (1927) 295. *pl. 48, f. 6, 12, 14, 15* (described, La Jolla formation).

Hypotype 15729; loc 1817; length (incomplete) 8.0 mm., altitude 5.3 mm.

This species was described from the Rose Canyon shale member of the La Jolla formation, near San Diego, California. It occurs in the Coalinga collections only from the Arroyo Hondo formation. This apparent stratigraphic difference is probably due to the apparent fact that both the Rose Canyon shales and the Arroyo Hondo formation were deposited in deeper and quieter water than the Domengine formation.

Corbula domenginica NEW SPECIES

PLATE 16, FIGURES 4, 8, 12

Corbula parilis "Gabb;" Arnold (1909) 13 (in part). *pl. 2, f. 2* (San Joaquin Coal Mine).—Arnold & Anderson (1910) 70. *pl. 24, f. 2* (San Joaquin Coal Mine).
Corbula dilatata Waring (1917) 92 (Arnold's figure cited in synonymy), (not *pl. 15, f. 2*).—Clark (1926) 114 (Coalinga).

Syntype 15730; loc. 7155; length (incomplete) 6.4 mm., altitude 4.4 mm.
Syntype 15731; loc. 7155; length 7.3 mm., altitude 4.0 mm.
Paratype 15732; loc. 7155; length (incomplete) 4.5 mm., altitude 3.3 mm.

DESCRIPTION.—Shell small, only moderately inflated; umbos central; ventral margin broadly rounded; anterior margin more sharply

rounded, straightening to form a slightly convex anterior dorsal margin; posterior margin produced, straight, sharply angulate at the ventral margin; a well-defined posterior umbonal ridge extending to the posterior ventral angulation, with a broad groove parallel to the ridge and immediately posterior to it; surface with irregularly developed, strong concentric undulations separated by round-bottomed interspaces; interior not seen.

COMPARISON.—*Corbula domenginica* resembles *C. rosecanyonensis* M. A. Hanna in outline and degree of inflation, but differs from that species in possessing a well-defined umbonal ridge and an umbonal groove immediately posterior to it. The sculpture of concentric undulations separated by round-bottomed interspaces also is in contrast to that of "large regularly rounded concentric ridges separated by rather deep V-shaped interspaces, some of which carry a fine interline" (M. A. Hanna 1927: 296), which is characteristic of *C. rosecanyonensis*. This species is more equilateral than *C. dilatata* Waring (renamed *C. complicata* Hanna), *C. dickersoni* Weaver & Palmer, or *C. tomulata* M. A. Hanna, and lacks the radial striations of *C. parilis* Gabb.

C. domenginica is known only from the carbonaceous strata at the San Joaquin Coal Mine.

Genus CUNEOCORBULA Cossmann 1886

GENOTYPE (by subsequent designation, ? Dall 1898): *Corbula biangulata* Deshayes. Eocene, Paris Basin, France.

Cuneocorbula Cossmann (1886: 49) was proposed as a section of *Corbula* for *Corbula biangulata* Deshayes and *C. angulata* Lamarck, both from the Eocene of the Paris Basin. The first valid designation of which the writer is aware is that of *C. biangulata* by Dall in 1898.

Corbula biangulata Deshayes (figured by Deshayes as *C. biangula*) was characterized by Gardner (1926b: 44) as a small, thin shell, much produced posteriorly, strongly bicarinate, feebly and irregularly sculptured.

Cuneocorbula was used by Dall and others as the subgeneric grouping for the forms here considered to belong to *Corbula* subgenus *Caryocorbula* Gardner. These species differ from *Cuneocorbula* in lacking the pronounced posterior prolongation and the biangulate rostrum, and in being strongly and regularly sculptured.

Cuneocorbula torreyensis (M. A. Hanna)

PLATE 16, FIGURES 16, 20, 21

Corbula torreyensis M. A. Hanna (1927) 296. *pl. 44, f. 6, 7, 8, 9, 10, 15, 16* (described, La Jolla formation).

Hypotype 15737; loc. A-1029; length 6.3 mm., altitude 3.1 mm
Hypotype 15738; loc. A-1029; length 3.8 mm., altitude 2 1 mm.
Hypotype 15739; loc. A-1029; length (incomplete) 3.5 mm., altitude 2.3 mm.

This remarkable little species is very similar to *C. biangulata* Deshayes, the type of *Cuneocorbula.*

Cuneocorbula griswoldensis NEW SPECIES

PLATE 16, FIGURES 18, 19

Holotype 15741; loc. A-1154; length (incomplete) 3.0 mm., altitude 2.0 mm.
Paratype 15742; loc. A-1154; length (incomplete) 4.5 mm., altitude 3.5 mm.

DESCRIPTION.—Shell small, elongate, subtrapezoidal, strongly rostrate; umbos small, anterior; posterior dorsal margin long, straight; anterior dorsal margin straight; anterior margin sharply rounded, the ventral margin broadly and irregularly rounded, the posterior margin short, straight; surface with a well-defined anterior umbonal ridge, a broad median inflation, a strong, prominent, and high posterior umbonal ridge to the posterior ventral margin, and a posterior dorsal umbonal ridge equally strongly developed; a well-defined groove separating the posterior ridges; sculpture consisting of poorly defined concentric ribs, not present on the posterior rostrum, and prominent lines of growth.

COMPARISON.—*C. griswoldensis* most closely resembles *C. torreyensis* (M. A. Hanna), but differs greatly from that species in the presence of the anterior ridge and median inflation, as well as in the possession of much stronger posterior ridges.

This species is known only from locality A-1154 at Griswold's Creek, near the western end of the Vallecitos syncline, where its association with *Pelecyora aequilateralis* (Gabb), *Potamides carbonicola* Cooper, and *Loxotrema turrita* Gabb suggests a brackish-water environment.

Family TEREDIDAE

Genus TEREDO Linnaeus 1758

GENOTYPE (by subsequent designation, Children 1822): *Teredo navalis* Linnaeus. Recent, northern seas of Europe.

Teredo SPECIES

Teredo sp. Dickerson (1916) 432 (between Domengine and Cantua creeks).

Fossil wood with unmistakable *Teredo* borings is abundant in two areas in the Domengine formation: the basal conglomerate of the Reef Ridge section, and throughout the formation in the region between Oil City and Domengine Ranch. There appear to be two species repre-

sented, one with long straight tubes ranging up to 10.0 mm. in diameter, the other with smaller, irregularly twisted tubes.

Subgenus **KUPHUS** Guettard 1770

TYPE SPECIES (by subsequent designation, ? Cox 1927): *Teredo polythalamia* (Linnaeus). Recent, East Indies, East Africa, Madagascar, and Red Sea (*fide* Cox).

The above subgeneric name and designation is given as of Cox (1927: 62). Herrmannsen (1847: 355) and Gray (1847b: 188) both give Guettard's name as *Cuphus*, Gray dating it from 1772, and Herrmannsen from 1774. For *Cuphus* Guettard 1772, *Kuphus* Gray 1840, Gray designated *Serpula polythalamia.*

Teredo (Kuphus) sp. aff. polythalamia (Linnaeus)

Irregularly shaped worm-like tubes with a median partition, on either side of which there is an inner circular tube, occur in the collections from Reef Ridge and the Vallecitos. These appear to be referable to the mud-boring subgenus *Kuphus,* in which the inner tubes serve as outlets for the siphons. According to Cox (1927: 62–64) it is impossible to distinguish the Eocene tubes from the Recent, so that it seems best to simply refer them to the Recent form.

The genus has not been previously reported from the California Tertiary. While this is probably due to failure to recognize their molluscan relationship, it is possible that the group is not represented in later horizons. The only Eocene horizon from which the species has been reported previously, as far as the writer is aware, is the Kirthar Group of India. In the Oligocene and Lower Miocene it was widespread in the eastern hemisphere, being known from the East Indies, India, Madagascar, Persia, and southern France (*fide* Cox, *op. cit.*).

Class SCAPHOPODA

Family DENTALIIDAE

Genus DENTALIUM Linnaeus 1758

GENOTYPE (by subsequent designation, Montfort 1810): *Dentalium elephantinum* Linnaeus. Recent, Amboyna and Philippine Islands.

The entire group of West American *Scaphopoda* has been but little studied and is in great need of a thorough revision before it will be of any practical use to the stratigrapher. At least four species of *Dentalium* are present in the Coalinga collections, only one of which is referable to any previously described West Coast Tertiary species. The

following Eocene species have been described from the Western horizons:

D. cooperii Gabb. There is but little doubt that Gabb's original description is based upon more than one species. The writer prefers to restrict this species to those forms which are characterized by the presence of fine longitudinal striations, as this is the group to which the specific name has most commonly been referred. The forms which are smooth throughout may be referred to *D. calafium* n. sp. (page 105), although Gabb does not mention the notched apex.

D. stentor Anderson & Hanna.

D. stramineum Gabb. Possibly a *Dentalium* (*sensu stricto*).

D. vacavillense Palmer. This species is characterized by being compressed between the convex and concave sides. This is a characteristic of the subgenus *Compressidens* Pilsbry & Sharp (1897: 123), but that subgenus is said to be "weakly sculptured, almost smooth." It is possible that *D. vacavillense* belongs to an ancestral section of this group.

Dentalium (Dentalium ?) stramineum Gabb

Dentalium stramineum Gabb (1864) 139. *pl. 21, f. 101* (described, Martinez, San Diego, and Curry's).—Dickerson (1916) 432, 447 (loc. 672).—Clark (1926) 115 (Coalinga).

This species is questionably referred to *Dentalium* (*sensu stricto*) although no specimens in which the apical area was preserved were available for study. The nature of the longitudinal ribbing is most suggestive of typical *Dentalium*, although the development of the ribbing is not well known as yet. The smallest apex examined shows 7 primary ribs, and the increase in strength of the inter-ribs until they equal the primary ribs leads to the development of at least 30 primary ribs and an almost equal number of inter-ribs.

Subgenus ANTALIS H. & A. Adams 1854

Type species (by subsequent designation, Pilsbry & Sharp 1897): *Dentalium entalis* Linnaeus. Recent, Atlantic coasts of Europe south to Spain, and Massachusetts to Bay of Fundy, North America.

Antalis is distinguished in the possession of a shell sculptured with longitudinal ribs or striae, at least in the young, often smooth in the adult, and in having a circular or polygonal outline. There may be a V-shaped notch at the apex, or a solic plug and a short tube or orifice. According to Pilsbry & Sharp (1897: 37) these apical characters are often not shown in the specimens.

Dentalium (Antalis) apicostatum NEW SPECIES

PLATE 16, FIGURE 25

Holotype 15747; loc. 672; length 11.4 mm., greatest diameter 1.7 mm., least diameter 0.5 mm.

DESCRIPTION.—Shell small, slender, but slightly curved, ovate in cross-section throughout; apical 2 mm. of shell ornamented by approximately 45–50 rounded longitudinal ribs of varying strength, generally with a strong rib alternating with a finer inter-rib; rest of shell smooth and polished.

COMPARISON.—*D. apicostatum* is characterized by having only the upper 2 mm. of the shell sculptured. Gabb's discussion of *D. cooperii* (Gabb 1864: 139. *pl. 21, f. 100*) suggests that that species may belong to the group of species of *Dentalium* which are characterized by the possession of a smooth apical region and longitudinal ribbing on the adult shell.

Subgenus **LAEVIDENTALIUM** Cossman 1888

TYPE SPECIES (by original designation): *Dentalium incertum* Deshayes. Eocene, Paris Basin, France.

Dentalium (Laevidentalium) calafium NEW SPECIES

PLATE 16, FIGURES 30, 31

? *Dentalium cooperi* Gabb; Stanton (1896) 1027 (New Idria).—Anderson (1905) 164 (Avenal sandstones).—Anderson (1908) 15 (north of Oil City).—Arnold (1909) 13 (southwest of Domengine's Ranch).—Arnold & Anderson (1910) 71 (southwest of Domengine's Ranch).

Syntype 15750; loc. A-1027; length (incomplete) 38.4 mm., greatest diameter 3.2 mm., least diameter 1.0 mm.
Syntype 15751; loc. A-1003 (Pine Canyon, Mount Diablo); length (incomplete) 7.6 mm., greatest diameter 1.7 mm., least diameter 1.0 mm.

DESCRIPTION.—Shell of medium size, slender, nearly straight, smooth and polished throughout; cross-section of shell round at both apex and aperture; apex with a slight notch on the convex side.

COMPARISON.—*D. calafium* may be distinguished from all described West Coast Tertiary species by the presence of the apical notch on the convex side of the shell. The smooth polished shell is sufficient to distinguish this species from all but *D. lighti* n. sp., which is oval in cross-section at the apical end.

Dentalium (Laevidentalium ?) lighti NEW SPECIES

PLATE 16, FIGURE 26

Dentalium sp. Anderson in Dumble (1912) 32 (Salt Creek).

Holotype 15752; loc. 1817; length (incomplete ?) 12.5 mm., greatest diameter 2.3 mm., least diameter 0.9 mm.

DESCRIPTION.—Shell small, short, stout for the length, rather strongly curved, smooth and polished; apical margin entire, ovate in cross-section, the shell rather thick; aperture round in section, the shell rather thin.

COMPARISON.—*D. lighti* resembles *D. calafium* in the smooth, polished surface of the shell, but is ovate in cross-section at the apical end, and lacks the notch which is characteristic of that species.

Named in honor of S. F. Light, professor of zoology at the University of California.

Family SIPHODENTALIIDAE

Genus CADULUS Philippi 1844

GENOTYPE (by subsequent designation, Herrmannsen 1846): *Cadulus ovulum* Philippi. Miocene to Recent, Mediterranean Sea.

Cadulus (?) NEW SPECIES

PLATE 16, FIGURE 32

Cadulus pusillus (Gabb); Dickerson (1916) 426, 427, 432, 447 (loc. 1817).

Figured specimen 15753; loc. 1817; length (incomplete) 3.8 mm., greatest diameter 0.9 mm., least diameter 0.4 mm.

Specimens of a small *Cadulus*-like form from locality 1817 differ from *C. gabbi* Pilsbry & Sharp (= *C. pusillus* (Gabb), not Philippi) in being ovate or elliptic in outline and more strongly inflated in the center of the shell. *C. meganosensis* Palmer is much more inflated. None of the specimens in the collection show the apical region, and the presence or absence of the numerous apical notches is unknown.

Meioceras Carpenter 1858, a Caecid gastropod with a similar outline, has a pointed apical plug.

Class CEPHALOPODA

Order NAUTILOIDEA

Family CLYDONAUTILIDAE

Genus ATURIA Bronn 1838

GENOTYPE (by virtual tautonomy, and subsequent designation, Herrmannsen 1846): *Nautilus aturi* Basterot. Burdigalian, Lower Miocene, France.

For a review of the genus *Aturia* and the West Coast species of the genus, the reader is referred to Schenck's "Cephalopods of the genus Aturia from western North America" (1931).

Aturia myrlae M. A. Hanna

PLATE 16, FIGURE 36

Aturia mathewsonii "Gabb"; Dickerson (1916) 434 (between Domengine and Cantua creeks).
Aturia myrli M. A. Hanna (1927) 331. *pl. 57, f. 1, 6* (described, La Jolla formation).—Clark. in M. A. Hanna (1927) 260 (Coalinga).
Aturia myrlae M. A. Hanna; Schenck (1931) 454. *pl. 67, 68; text-f. 4–3, 4–19.*

Hypotype 15877; loc. 1817; altitude (incomplete) 12.8 mm., width of outer whorl 6.8 mm.

As indicated by the measurements given above, Hypotype 15877 is the smallest specimen of this genus as yet reported. An examination of the lateral lobes in the earliest stage of growth visible shows that the pinched-in character of the approximating lateral lobes has been developed and that the lobes are parallel-sided and situated near the venter. This condition seems to confirm the specific distinctness of *A. myrlae,* as even more mature specimens of *A. mathewsonii* Gabb (1864: 59. *pl. 17, f. 31*) and *A. kerniana* Anderson & Hanna (1925: 49. *pl. 6, f. 8; text-f. 1, 2*) show blunt, parallel-sided lateral lobes.

Two specimens of this species are in the collections from locality 2291 in the Domengine formation. Hypotype 15877 is from the Arroyo Hondo formation and is associated at loc. 1817 with abundant fragments of the outer shell of much larger individuals.

Class GASTROPODA

Subclass OPISTHOBRANCHIATA

Order TECTIBRANCHIATA

Family ACTEONIDAE

Genus TORNATELLAEA Conrad 1860

GENOTYPE (by monotypy): *Tornatellaea bella* Conrad. Eocene, Claiborne, Alabama.

Tornatellaea effingeri NEW SPECIES

PLATE 16, FIGURES 22, 23

Holotype 15754: loc. 1817; length (incomplete) 4.5 mm., diameter 2.5 mm.

DESCRIPTION.—Shell small; whorls about five (nuclear whorls broken), flat-sided, first one and a half whorls smooth, the rest ornamented by narrow thread-like ribs separated by flat, wide interspaces five to six times as wide as the ribs; about 18 ribs on the body-whorl; suture appressed; aperture oval with two strong columellar plications on the inner lip, which is slightly callused.

Comparison.—*T. effingeri* differs from all described West Coast species in the presence of very narrow ribs separated by wide interspaces, rather than broad flat ribs separated by narrow punctate interspaces. The flat-sided whorls are also distinctive. Named in honor of Mr. William Effinger, former graduate student at the University of California.

Tornatellaea new species

Specimen 15755; loc. 1817.

One well preserved immature specimen of a minute *Tornatellaea* is found in the collections from the Arroyo Hondo formation. There are 3 whorls, only the body-whorl being ornamented. The body-whorl is globose, tabulated at the suture, ornamented by broad flat-topped ribs separated by narrow punctate interspaces. The ribs are obsolete on the top of the whorl, but well developed on the base. The aperture is round, the inner lip callused and bearing 2 sharp columellar plications.

This form is too immature to be named. It appears to differ from all described West Coast species in the obsolete character of the ribbing on the upper part of the body-whorl.

Genus KLEINACTEON new genus

Genotype: *Acteon moodyi* Dickerson. Domengine formation, Eocene, California.

The genus *Acteon* Montfort (1810: 315) type (by original designation) *Voluta tornatilis* Gmelin (= *V. tornatilis* Linnaeus), possesses a heterostrophic nucleus and an imperforate shell. The Domengine species "*Acteon*" *moodyi* has a smooth, somewhat naticoid nucleus of two whorls, and the base of the shell possesses a well-developed umbilicus. The columella is marked by a small, poorly defined plait, which is similar in position to but much less strongly developed than the plait on *Acteon* (*sensu stricto*).

The umbilicate shell of *Kleinacteon* is similar to that of the recent *Kleinella* A. Adams (1860: 302) type *K. cancellaris* A. Adams, but that species lacks the columellar plait.

The absence of the heterostrophic nucleus makes the reference of this genus to the family *Acteonidae* questionable.

Judging from the figure, *Acteon quercus* Anderson & Hanna (1925: 141. *pl. 8, f. 1*) may possibly be a *Kleinacteon*.

Kleinacteon moodyi (Dickerson)

PLATE 16, FIGURE 24

? *Acteon* sp. indet. Arnold (1909) 13 (Reef Ridge).—Arnold & Anderson (1910) 71 (Reef Ridge).
Acteon moodyi Dickerson (1916) 432, 448, 488. *pl. 38, f. 10a, 10b* (described, loc. 672).—Anderson & Hanna (1925) 141 (Tejon record based on *A. quercus*).
Acteon "*moodeyi*" Clark (1926) 115 (Coalinga).

Holotype 31177; loc. 672; length 8.7 mm., diameter 5.0 mm.

This species was described from loc. 672, north of Coalinga. The spiral ribs are not punctate, and the growth-lines are prominently developed in the interspaces, which are approximately two thirds as wide as the ribs.

A poorly preserved specimen of a new species of *Acteon* from loc. 1817 has punctate spiral ribbing and an imperforate shell. The nuclear whorls are absent, but it does not appear to be a *Kleinacteon*.

Family SCAPHANDRIDAE

Genus SCAPHANDER Montfort 1810

GENOTYPE (by original designation): *Bulla lignaria* Linnaeus. Recent, British Coast, Mediterranean Sea, and Scandinavia (Reeve).

Subgenus MIRASCAPHA Stewart 1927

TYPE SPECIES (by original designation): *Cylichna costata* Gabb. Eocene, California.

Scaphander (Mirascapha) costatus (Gabb)

PLATE 16, FIGURES 29, 35

Cylichna costata Gabb (1864) 143. *pl. 21, f. 107* (described).—Turner & Stanton (1894) 95 (New Idria).—Stanton (1896) 1027 (New Idria).—Turner in Anderson (1908) 10 (New Idria).—Anderson (1908) 13 (Salt Creek).—Anderson in Dumble (1912) 32 (Salt Creek).—Dickerson (1916) 426, 427, 432, 449 (between Domengine and Cantua creeks).
Scaphander "cf. *costata*" (Gabb); Clark (1926) 116 (Coalinga).
Scaphander "*costata*" (Gabb); Clark in M. A. Hanna (1927) 260 (Coalinga).—Merriam & Turner (1937) 100 (Lillis Ranch).
Scaphander (*Mirascapha*) *costatus* (Gabb); Stewart (1927) 437 (lectotype and partial synonymy).

Hypotype 15756; loc. 672; length 15.2 mm., diameter 7.3 mm.

This species, while widely distributed throughout the Middle Eocene of the Coalinga region, is rather rare at all localities, and many of the references cited above probably refer to the much more abundantly represented *Cylichnina tantilla* (Anderson & Hanna).

Genus CYLICHNINA Monterosato 1884

GENOTYPE (*fide* Stewart 1927): *Bulla umbilicata* Montagu (not Roeding) = *Cylichnina strigella* Lovén. Recent, Mediterranean and Adriatic seas and Atlantic Ocean (Bucquoy: Dautzenberg & Dollfuss).

Cylichnina tantilla (Anderson & Hanna)

PLATE 16, FIGURES 28, 33, 39

Cylichna costata "Gabb"; Arnold (1909) 13, 15. *pl. 4, f. 19* (Reef Ridge, north of McLure Valley).—Arnold & Anderson (1910) 71, 72. *pl. 26, f. 19* (Reef Ridge, north of McLure Valley).

? *Bullaria hornii* (Gabb); Dickerson (1916) 426, 432, 448 (in part) (between Domengine and Cantua creeks).

Cylichnella tantilla Anderson & Hanna (1925) 140. *pl. 7, f. 4, 8, 9* (described, Tejon).

Cylinchnina tantilla (Anderson & Hanna); Stewart (1927) 439–41. *pl. 27, f. 2, 3, 4* (synonymy).

Hypotype 15757; loc. 672; length 14.8 mm., diameter 5.8 mm.
Hypotype 15758; loc. 672; length 8.5 mm., diameter 3.4 mm.
Hypotype 15759; loc. 672; length 5.8 mm., diameter 2.2 mm.

It is possible that Dickerson's record of *Bullaria hornii* (Gabb) from the Coalinga Eocene may be based upon specimens of *Scaphander costatus* (Gabb), in which event his records of "*Cylichna*" *costata* would be based upon this species.

Genus CYLICHNA Lovén 1846

GENOTYPE (by subsequent designation, Gray 1847): *Bulla cylindrica* Montagu. Recent, seas of Europe.

Subgenus CYLICHNOPSIS Cossmann 1904

TYPE SPECIES (by original designation): *Cylichna acrotoma* Cossmann. Eocene, Claiborne, Gulf Coast.

Cylichna (?) (Cylichnopsis) compara NEW SPECIES

PLATE 16, FIGURE 27

Holotype 15760; loc. 7155; length 6.4 mm., diameter 2.9 mm.

DESCRIPTION.—Shell small, cylindric, moderately stout; spire involute, the apex perforate, subtruncate, the perforation almost closed by the callus of the inner lip; aperture long, broader anteriorly and posteriorly; outer lip simple; inner lip with a thin callus throughout its entire length, the callus being reflected well over the base of the shell, and bearing a slight fold anteriorly; surface sculptured by spiral grooves which are most prominent anteriorly, but are moderately prominent posteriorly, being only microscopically developed on the center of the shell.

COMPARISON.—*Cylichna* (?) *compara* differs from *Cylichnina tantilla* (Anderson & Hanna) mainly in the nature of the callus on the inner lip, which is reflected over and almost closes the apical perforation, and which is anteriorly reflected well over the base of the shell and has a small fold.

Cylichna (*Cylichnopsis*) *acrotoma* Cossmann (1893: 50. *pl. 1, f. 40; pl. 2, f. 1*) from the Claiborne Eocene of the Gulf Coast, is a somewhat similar species, which differs, however, in possessing a sharply truncated apex, and in lacking the development of the callus on the base of the shell. The callus, however, does bear a slight fold.

Family AKERIDAE

Genus AKERA Müller 1776

GENOTYPE (by tautonomy): *Akera bullata* Muller = *Bulla akera* Gmelin. Recent, coasts of Denmark (Reeve).

This is the "*Acera* Müller" of Cossmann (1895: 103), not of Cuvier 1817, and Cossmann's original spelling of the family name was *Aceriidae*.

Akera maga NEW SPECIES

PLATE 16, FIGURES 34, 40, 41

Holotype 15761; loc. A-1281; length 9.5 mm., diameter 5.5 mm.
Paratype 15762; loc. A-976; length 15.0 mm., diameter 7.7 mm.

DESCRIPTION.—Shell of moderate size, ovate-cylindric, thin; spire low, projecting; aperture long, dilated anteriorly; outer lip not touching the spire, forming a decided groove between the callus of the inner lip and the preceding whorl; surface sculptured by numerous distant, incised grooves which, when crossed by the growth lines, give the surface a cancellate appearance.

COMPARISON.—This is the first species referable to this genus which has been recognized in the West Coast Tertiary. It may be at once distinguished from other described cylindric gastropods from this region by the pronounced groove between the aperture and the preceding whorl.

The largest specimen in the collections reaches a length (incomplete) of 21.0 mm., and a diameter of 11.5 mm. All the specimens in the collections are from the Reef Ridge section.

Family PHILINIDAE

Genus MEGISTOSTOMA Gabb 1864

GENOTYPE (by monotypy): *Megistostoma striatum* Gabb = *Bullaea gabbiana* Stoliczka. Middle Eocene, California.

Megistostoma gabbianum (Stoliczka)

PLATE 17, FIGURES 1, 2, 3

Megistostoma "striata" Gabb (1864) 144. *pl. 21, f. 108, a, b* (described, Martinez).—Dickerson (1916) 433, 450 (between Domengine and Cantua creeks).—Clark (1926) 115 (Coalinga). Not *Bullaea striata* Deshayes (1824) 37. *pl. 5, f. 1, 2, 3* (= *Megistostoma*).
Bullaea gabbiana Stoliczka (1868) 434 (new name).
Philine (Megistostoma) gabbi Cossmann (1895) 127 (new name).
Megistostoma gabbianum (Stoliczka) Stewart (1927) 441, 442. *pl. 26, f. 1, 2* (holotype and synonymy).
Megistostoma "caminoensis" M. A. Hanna (1927) 330. *pl. 57, f. 9, 10* (described, La Jolla formation).—Turner (1938) 68. *pl. 20, f. 15* (closely resembles *M. gabbianum* (Stoliczka)).

Hypotype 15763; loc. 672; altitude 9.0 mm., anterior-posterior diameter 21.0 mm., minimum diameter 17.7 mm.
Hypotype 15764; loc. A-975; altitude 8.7 mm., anterior-posterior diameter 21.0 mm., minimum diameter 16.2 mm.
Hypotype 15765; loc. 1817; altitude (slightly crushed) 6.0 mm., anterior-posterior diameter 18.7 mm., minimum diameter 14.0 mm.

Stewart's figure of Gabb's holotype specimen (Stewart 1927: *pl. 26, f. 1*) shows that the original figure of this species was defective in that the anterior end is rounded, rather than almost pointed, the posterior extremity of the outer lip further produced, and the region of the spire not as greatly produced parallel to the posterior extremity. Abundant material indicates that these features of the outline are very variable. The callus on the inner lip may or may not be longitudinally striated, and in the majority of cases striae are absent. The statement that the elevated striae "are usually grooved in the middle" holds true, but in many cases, including the holotype of *M. caminoense* M. A. Hanna; these striae can be seen to divide along the line of grooving and separate into distant ungrooved riblets. They are slightly less regularly spaced than is indicated in Gabb's view of the surface of the shell. The material from the Coalinga region fully embraces the variation in outline and characters which have been held to separate *M. gabbianum* and *M. caminoense.*

Subclass STREPTONEURA

Order PECTINIBRANCHIATA

Suborder TOXOGLOSSA

Family TEREBRIDAE

Genus TEREBRA Bruguière 1789

GENOTYPE (by monotypy): *Buccinum subulatum* Linnaeus. Recent, Indo-Pacific.

The apertural features of neither of the species which are referred to this genus are sufficiently well preserved to permit subgeneric or sectional determination.

Terebra californica Gabb

PLATE 16, FIGURE 38

Terebra californica Gabb (1869) 162. *pl. 27, f. 41* (described, "Tejon Group, Martinez").—Dickerson (1916) 434, 453 (in part) (loc. 672) (not 427, loc. 1817).—Stewart (1927) 424, *pl. 26, f. 5* (holotype and synonymy). Not "*Terebra californica* Gabb;" Anderson & Hanna (1925) 82. *pl. 8, f. 18* (type Tejon).

Hypotype 15766; loc. 672; length (incomplete) 8.5 mm., diameter 2.8 mm.

Four specimens of *Terebra* representing this species occur in the collections. There are 27 axial ribs on the body-whorl of the specimen figured. The whorls are broadly concave immediately below the sutural collar.

The specimen figured by Anderson & Hanna from the type Tejon appears to possess a considerably smaller number of axial ribs and a more sharply delimited sutural collar. It probably does not represent this species.

Terebra NEW SPECIES

PLATE 16, FIGURE 37

Terebra californica "Gabb;" Dickerson (1916) 427, 434, 453 (in part) (loc. 1817).

Figured specimen 15767; loc. 1817; length (incomplete) 6.3 mm., diameter 2.1 mm.

A single poorly preserved specimen of a *Terebra* from loc. 1817, Capay stage, is in the collection. The body-whorl is ornamented by 14 broad, flat-topped axial ribs which do not appear to have crossed the sutural collar. The base of the body-whorl was apparently long, the columella well callused and bearing a single plication.

T. californica has a greater number of axial ribs which are also present on the sutural collar. *T. wattsiana* Cooper,* from the Capay horizon at Marysville Buttes, is known from a single specimen only, but is described as possessing approximately 50 close-set riblets on the body-whorl.

Family TURRIDAE

Many features combine to make the study of the *Turridae* the most difficult and perplexing of all the Molluscan families. The large number of generic and specific units, their generally short geologic range, the great nomenclatorial confusion which exists, and the tendency of the workers on the Recent groups to base much of their subfamily and generic criteria on the nature of the opercular features, all tend to make a satisfactory classification of the fossil species virtually impossible at the present time.

* Cooper (1894) 39. *pl. 1, f. 1.*—Description reprinted in Dickerson (1913: 281. *pl. 11, f. 10*).

The *Turridae* are carnivorous animals occupying a great range of variation in ecologic conditions, from the low tide-line almost to the abyssal zone. As is characteristically true of carnivorous types, the number of individuals is small in comparison with the herbivorous types.

No attempt is here made to review adequately the West Coast Eocene *Turridae*, and attention has been directed solely to those species which occur in the collections from the Coalinga district. It has not been found practical to attempt to establish the subfamily groupings of the genera here represented.

Arnold's species, *Pleurotoma domenginei* (Arnold 1909: 14, 52. *pl. 4, f. 16.* Domengine's Ranch), from the Domengine formation, is not represented in our collections and is therefore not evaluated here. His *P. guibersoni* (Arnold 1909: 14, 54. *pl. 4, f. 20.* Domengine's Ranch) is not a member of the *Turridae*, and *Fusinus ucalius* n. sp. (page 137) may prove to be synonymous.

Genus FUSITURRICULA Woodring 1928

GENOTYPE (by original designation): *Turris (Surcula) fusinella* Dall. Recent, Gulf of Panama.

Subgenus CRENATURRICULA NEW SUBGENUS

TYPE SPECIES: *Surcula crenatospira* Cooper. Eocene, Capay horizon, California.

The Eocene species which appear to be referable to *Fusiturricula* are in general larger and stouter than in the later species of this genus, the anal sinus somewhat shallower and the outer lip does not project as far forward. They are represented in the California Eocene deposits by *Fusiturricula (Crenaturricula) crenatospira* (Cooper) and a new subspecies. *Pleurotoma dentata* Lamarck, Lutetian of the Paris Basin, is a *Crenaturricula*, as is possibly also *Pleurotoma michelini* Deshayes. *Pleurotoma keelei* Edwards of the English Eocene, judging from the illustration, is similar.

Knefastia Dall (1919: 3) type (by original designation), *Pleurotoma olivacea* Sowerby, has a shorter and wider anterior canal, a narrower and somewhat deeper anal sinus, and a different nucleus.

Cooper's original description and figures of his species are defective, and if in the future any doubt arises as to the identification of the form here figured, it should nevertheless be considered to represent the type species of *Crenaturricula*.

Fusiturricula (Crenaturricula) crenatospira (Cooper)

PLATE 17, FIGURES 4, 5

Surcula crenatospira Cooper (1894) 39. *pl. 1, f. 2, 3, 4* (described, Marysville Buttes).—Dickerson (1913) 278. *pl. 11, f. 4* (Marysville Buttes).
Turris (*Surcula*) *crenatospira* Cooper; Clark (1921) 159 ("Meganos," N. of Coalinga).

Topotype 12166; loc. 1853 (Marysville Buttes); length 37.0 mm., diameter 14.5 mm.

This species is represented in the collections from locality 1817, Arroyo Hondo formation, by a single poorly preserved specimen. In its typical development it appears to be confined to and diagnostic of the Capay stage.

Fusiturricula (Crenaturricula) crenatospira (Cooper) domenginica NEW SUBSPECIES

PLATE 17, FIGURES 6, 7

Holotype 15768; loc. 7002 (Llajas formation, Simi Valley); length (incomplete) 47.5 mm., diameter 21.6 mm.
Paratype 15769; loc. 3304 (Llajas formation, Simi Valley); length (incomplete) 26.6 mm., diameter 14.7 mm.

DESCRIPTION.—Shell relatively large, moderately slender; nucleus and early post-nuclear whorls missing; aperture long, narrow; posterior sinus broad, moderately deep; canal long, straight, the anterior end missing; whorls angulate, the upper portion concave to a linear suture, the lower portion almost parallel to the axis of the shell, slightly concave; spiral sculpture consisting of primary, secondary, and tertiary riblets present only on the anterior portion of the whorl, being obsolete on the shoulder; middle of the body-whorl marked by 3 strong primary ribs a fairly strong secondary rib between each pair, separated from the primary by a microscopic tertiary; approximately 6 tertiary threads between the angulation of the whorl and the first primary; canal ornamented by numerous secondary and tertiary riblets; 2 primary and a secondary inter-rib present on the anterior portion of the spire-whorls; axial sculpture obsolete, reflected in a row of strong, horizontally flattened nodes along the angle of the whorl; 12 nodes on the body-whorl and 10 on the penultimate whorl of the holotype.

COMPARISON.—*F. crenatospira domenginica* differs from *F. crenatospira* (*sensu stricto*) in the obsolete nature of the axial sculpturing, which is present as swollen areas below the nodes on the typical species. Although Cooper's description of his species mentions that there are about 9 nodes on each whorl, the majority of topotype specimens available reveal only 7 on the body-whorl, while the Do-

mengine species possesses 10 to 12. The shell in *domenginica* is also more slender in proportion to the height.

This subspecies is not rare in the Domengine formation in the Vallecitos section, and is represented by a single specimen from the Reef Ridge area, but is not known from the type section north of Coalinga.

Genus EOPLEUROTOMA Cossmann 1889

GENOTYPE (by original designation): *Pleurotoma multicostata* Deshayes. Eocene, Paris Basin, France.

The species here referred, for want of a better systematic position, to this genus resembles several species referred to this group by Cossmann & Pissarro (1913: *pl. 51, 52*, in part) much more closely than it does the type species. It also is somewhat similar to *Pleurotoma depygis* Conrad, from the Claiborne, the type species by subsequent designation, Cossmann 1906, of *Eodrillia* Casey (1904: 159) which Cossmann has considered synonymous with his genus.

Eopleurotoma (?) traski NEW SPECIES

PLATE 17, FIGURE 9

Holotype 15770; loc. A-976; length (incomplete) 17.2 mm., diameter 7.6 mm.

DESCRIPTION.—Shell of medium size, moderately slender, of 9 postnuclear whorls (nucleus broken) which are strongly convex and angulate, sculptured by 9 swollen axial ribs strongly developed on the anterior portion of the whorl and absent from the posterior portion; axial ribbing obsolete on the body-whorl; spiral sculpture consisting of numerous microscopic threads on the posterior shoulder and 3 strong spirals with one or two finer inter-ribs on the anterior part of the whorl; the strong spirals, where they cross the axials on the spire, tending to produce minor angulations in the outline of the whorl; 3 strong spirals on the center of the body-whorl and numerous low, subobsolete spirals on the base and canal; suture appressed, linear, somewhat irregular due to the axial sculpturing; aperture slender; outer lip thin; posterior notch deep, rounded, the apex on the shoulder of the whorl; anterior canal of moderate length, slightly recurved, a well-developed siphonal fasciole present.

COMPARISON.—The species here named *Eopleurotoma traski* is rather similar to *Pleurotoma dentata* Lamarck of the Parisian Eocene. However, the posterior notch on that species is narrower and slightly more anterior than on the California species. *Pleurotoma* Lamarck (1799: 73; sole species *Murex babylonius* Linnaeus), is a subjective

synonym of *Turris* Bolten; Roeding (1798: 123). The type species of both genera is *Murex babylonius* Linnaeus, a species characterized by the "fluted" nature of the interior of the shell due to the presence of sharp, raised, revolving threads. Hedley (1922: 214) dates the generic name *Turris* from Müller (1766: 129). This reference is not available at the present time. Cossmann & Pissarro (1913: *pl. 51*, sp. 223 bis 11) refer Lamarck's species to the genus *Surcula* H. & A. Adams (1853: 88). This name was proposed as a substitute name for *Turricula* Schumacher (1817: 217), not Klein 1753. Klein's name, being pre-Linnaean, does not affect Schumacher's. The type of *Turricula*, by monotypy, is *T. flammea* Schumacher = *Turris javanus* Bolten (not Linnaeus or Gmelin) =*Murex tornatus* Dillwyn (not *Turris tornatus* Bolten). This is a smooth shell with a channeled area near the suture. *Orthosurcula* Casey (1904: 151), type (by subsequent designation, Gardner 1935) *Pleurotoma longiforma* Aldrich, is very closely related. The several species referred by Gardner (1935: 215–220. *pl. 20*) to this genus are not congeneric and none appears correctly assigned generically.

Named in honor of Dr. Parker D. Trask of the United States Geologic Survey, in appreciation of many valuable suggestions made in the field.

INCERTAE SEDIS

"Turricula" holwayi (Dickerson)

Surcula holwayi Dickerson (1913) 279. *pl. 11, f. 9.*

Surcula holwayi was described by Dickerson from a fragment lacking the apical whorls and all trace of apertural features. Specifically identical material from loc. 1817 is too poorly preserved to furnish any additional information as to the systematic position of this species.

Genus PLEUROFUSIA de Gregorio 1890

GENOTYPE (by original designation): *Pleurofusia longirostropsis* de Gregorio. Eocene, Claiborne, Alabama.

Pleurofusia fresnoensis (Arnold)

PLATE 17, FIGURES 15, 16

Pleurotoma fresnoensis Arnold (1909) 14, 53. *pl. 4, f. 23* (described, southwest of Domengine's Ranch).—Arnold & Anderson (1910) 71. *pl. 26, f. 23* (southwest of Domengine's Ranch).—Anderson in Dumble (1912) 32 (Salt Creek).

Turris fresnoensis Arnold; Dickerson (1916) 427, 434, 453 (loc. 1817) (not *pl. 37, f. 8*).—Clark (1921) 159 ("Meganos" north of Coalinga).

Surcula fresnoensis (Arnold); Anderson & Hanna (1925) 87 (from north of Coalinga, not at Tejon).

Surcula clarki Dickerson (1913) 278. *pl. 11, f. 3* (described, Marysville Buttes).—Dickerson (1916) 434, 452 (loc. 672).—Clark (1926) 116 (Coalinga).

? *Pleurofusia raricostata* (Gabb); Stewart (1927) 415, 416. *pl. 27, f. 13* (part only, not *pl. 27, f. 14*, the lectotype).

Hypotype 15771; loc. 672; length 12.8 mm., diameter 4.9 mm.
Hypotype 15772; loc. 672; length 11.0 mm., diameter 4.5 mm.

Arnold's original figure is too poor to permit certain identification; however, the larger specimen figured (hypotype 15771) was compared with Arnold's type by the late Dr. Dall, who confirmed the identification.

There are 7 or 8 nodes on each whorl, the area above the nodes being most commonly concave, and ornamented directly below the suture by a strong spiral line.

Specimens from the Arroyo Hondo formation (loc. 1817) average 8 or 9 nodes on the whorl and possess 4 strong spirals on the area below the angle of the whorl. *Pleurofusia lindavistaensis* (M. A. Hanna*) is a closely related species, which differs in lacking the strong sutural spiral; the area above the angle of the whorl is less concave, and slightly more strongly spirally sculptured.

Stewart (1927: 415–417. *pl. 27, f. 13, 14*) in his discussion of "*Pleurofusia*" *raricostata* (Gabb) has figured two distinct forms as representing that species (Stewart 1930: 16). He states that "the other specimen figured (fig. 13) is closer to Gabb's size mark, and may actually be the holotype," but designates the other specimen figured (*f. 14*) as the lectotype. Judging from the figure, the specimen shown in *f. 13* may be referable to *P. fresnoensis*. However, as Stewart has fixed Gabb's specific name on the other specimen, Arnold's name does not become a synonym of Gabb's. The lectotype does not appear to be a *Pleurofusia*.

Genus EOSURCULA Casey 1904

GENOTYPE (here designated): *Eosurcula moorei* (Gabb). Eocene, Texas.

Cossman (1906: 221) and Dall (1918b: 326) both state that *E. moorei* is the first species on Casey's list, but do not formally designate it as the type. As far as the writer is aware no type has been designated by other authors.

Eosurcula capayana NEW SPECIES

PLATE 17, FIGURES 12, 13

Syntype 15900; loc. 1817; length 35.5 mm., diameter 9.0 mm.
Syntype 15901; loc. 1817; length (incomplete) 15.3 mm., diameter (incomplete) 4.7 mm.

DESCRIPTION.—Shell moderately large, fusiform, of approximately 8 whorls; nucleus décolleté on all specimens; spire-whorls medially

* M. A. Hanna (1927) 325. *pl. 56, f. 3, 7, 8*; as *Surcula lindavistaensis*.

angulate, the area posterior to angulation slightly concave, forming a smooth shoulder sloping to the appressed, slightly channeled suture; angulation marked by a strong spiral rib, with a second primary spiral approximately equidistant between the angulation and the succeeding whorl, with a secondary spiral adjoining on either side; body-whorl with a third primary equally distant anteriorly from the second, marking the edge of the base of the whorl; base and long anterior canal with numerous alternating secondary and tertiary spirals; aperture and anterior canal almost twice as long as the spire, very slender; outer lip simple; anal sinus moderately deep, high on the shoulder of the whorl.

COMPARISON.—The long and slender aperture and anterior canal will serve to distinguish this from all other described West American Eocene *Turridae* which lack axial sculpturing.

Genus MICROSURCULA Casey 1904

GENOTYPE (by original designation): *Microsurcula nucleola* Casey. Eocene, Lower Claiborne, Louisiana.

This generic name is virtually a *nomen dubium*, as the type species has not been figured. Its use here is based upon the similarity of *Microsurcula* (?) *ligna* n. sp. to specimens labelled *Microsurcula* n. sp. aff. *intacta* Casey from the Oligocene of the Gulf Coast of the United States in the collections of the University of California.

Microsurcula (?) ligna NEW SPECIES

PLATE 17, FIGURE 10

Holotype 15773; loc. 7155; length (incomplete) 6.5 mm., diameter 2.8 mm.

DESCRIPTION.—Shell small, of 5 whorls; nucleus and first post-nuclear whorl missing; whorls convex, sculptured with 10 sinuous, swollen, axial ribs and 10 or 11 rounded spiral threads; axial ribs most strongly developed below the appressed sutural collar and forming an angulation to the whorl, on the body-whorl tending to become obsolete toward the base; spiral sculpturing of 4 or 5 strong anterior threads crossing the axials, and numerous finer threads on the shoulder and sutural collar; 29 threads on the body-whorl and anterior canal; aperture elongate; canal short, straight, and rather wide; outer lip thin; posterior notch broadly rounded, the apex occurring just above the angle of the whorl; inner lip slightly resorbed, smooth.

COMPARISON.—*Microsurcula* (?) *ligna* appears to be unique among the Eocene turrids of the West Coast. The nature of the sculpturing

is somewhat suggestive of *Pleurofusia fresnoensis* (Arnold), but in that species the axial ribs do not extend as high on the whorl and the shoulder is broader and more pronounced.

Genus TRYPANOTOMA Cossman 1893

GENOTYPE (by original designation): *Pleurotoma terebriformis* Meyer. Eocene, Claiborne, Gulf Coast.

The large, paucispiral nucleus appears to characterize this genus, and to be sufficiently distinctive to separate it completely from *Asthenotoma* Harris & Burrows (1891: 113; new name for *Oligotoma* Bellardi 1875, not Westwood 1836), of which Cossmann (1896: 109) considered *Trypanotoma* a subgeneric group.

Trypanotoma stocki (Dickerson)

PLATE 17, FIGURE 14

Turris stocki Dickerson (1916) 434, 453, 499. *pl. 42, f. 5* (described, loc. 672).—Clark (1926), 116 (Coalinga).
Gemmula stocki (Dickerson); Anderson & Hanna (1925) 93 (from north of Coalinga, Tejon record based on *Gemmula abacta* Anderson & Hanna).

Topotype 15774; loc. 672; length 10.2 mm., diameter 3.6 mm.

The type (U. C. Coll. no. 11821) is the largest individual referable to this species in the collection, but is somewhat worn and décolleté, which resulted in some inaccuracies in the original description; the suture is linear, but is not impressed, in fact is so obscure as to be almost invisible on well-preserved material; the first of the spiral lines above the nodose row is most commonly adjacent to that row, and separated from the posterior spiral by a fairly wide, smooth area. The aperture is moderately broad; the outer lip simple, although lirate deeply within, and the posterior notch culminates at a point marked by the line of spiral nodes; the inner lip is thinly callused; the canal is short, broad, and very slightly recurved, with the development of an incipient siphonal fasciole.

The nature of the sculpturing and of the aperture is almost identical with that observed on *T. terebriformis* (Meyer), the genotype.

Genus GEMMULA Weinkauff 1876

GENOTYPE (by subsequent designation, Cossmann 1896): *Pleurotoma gemmata* Hinds in Reeve. Recent, Indo-Pacific.

Gemmula appears to be one of the most persistent of the turrid genera. It is represented in the Eocene of California by several species, although a number of species also have been incorrectly referred to this group. Specimens of *Gemmula gemmata* have not been available

for study, but specimens of *Gemmula graeffei* (Weinkauff) from the Viti Islands have been noted. This species was considered by Tryon (1884: 173. *pl. 4, f. 51, 54*) to be "doubtfully distinct" from *gemmata*. The nucleus is distinguished by the possession in the later stages of axial ribbing which is first protractive and later retractive. The sinus is relatively deep, with its apex at the line of nodes on the angulation of the whorl. Similar axial ribbing occurs on the nucleus of several California species, although in most cases it is not as markedly retractive in the later stage. The following four species appear to be referable to *Gemmula*:

Gemmula wattsi Anderson & Hanna (1925: 94).

Gemmula abacta Anderson & Hanna (1925: 92. *pl. 7, f. 6, 7; pl 8, f. 11*).

Gemmula tumata M. A. Hanna (1927: 317. *pl. 51, f. 3, 8, 10*).

Gemmula violeta M. A. Hanna (1927: 318. *pl. 52, f. 3, 4, 8, 10, 13*).

"*Gemmula*" *diabloensis* Clark & Woodford (1927: 107. *pl. 19, f. 3, 4*) is not a *Gemmula*, the apex of the anal sinus being on the shoulder well above the line of nodes, and the nucleus lacking axial sculpturing. "*Turris*" *stocki* Dickerson, referred to *Gemmula* by Anderson & Hanna (1925: 93), is here considered to be a *Trypanotoma*. Nuclear whorls of *Gemmula encinalis* Anderson & Hanna (1925: 93. *pl. 8, f. 10*) and of *Gemmula fasteni* Weaver & Palmer (1922: 42. *pl. 12, f. 1, 4*) were not available for study.

Gemmula wattsi Anderson & Hanna

Surcula monilifera Cooper (1894) 39, 40. *pl. 2, f. 28, 29* (described, Marysville Buttes).
Turris monolifera (Cooper); Dickerson (1913) 275. *pl. 11, f. 1* (Marysville Buttes, original description reprinted).—Dickerson (1916) 427, 434, 453 (loc. 1817), 434 (loc. 672 in error).
Turris (Pleurotoma) monolifera Cooper; Clark (1921) 159 ("Meganos," N. of Coalinga).—Not *Turris monilifera* Pease (1860) 398; nor *Pleurotoma monilifera* Pease (1869) 68 (= *Gemmula*).
Gemmula wattsi Anderson & Hanna (1925) 94 (new name, not at Tejon).

This species appears to be characteristic of the Capay stage and in the Coalinga district occurs only in the collections from loc. 1817.

Gemmula cf. violeta M. A. Hanna

Cf. *Gemmula violeta* M. A. Hanna; Clark in M. A. Hanna (1927) 260 (Coalinga).

A single specimen of *Gemmula* in the Domengine collections from loc. A-973 is too poorly preserved to permit definite specific identification.

DOMENGINELLA NEW GENUS

GENOTYPE: *Turris claytonensis* Gabb = *Surcula gesteri* Dickerson. Eocene, Domengine horizon, California.

Domenginella is proposed for a genus of small turrids the type of which is almost identical in shape and sculpturing with *Scobinella*

coelata Conrad, the monotype species of *Scobinella* Conrad 1848, but differs from that genus in possessing a smooth columella, which lacks all trace of the strong Mitra-like plications characterizing Conrad's genus. The genotype appears to be the only known California species referable to this genus, but *Pleurotoma microcheila* and possibly *Pleurotoma dissimilis*, *Pleurotoma pupa*, *Pleurotoma dilinum*, all described by F. E. Edwards from the British Eocene, appear to be referable to the genus. The first three of the above species were referred by Cossmann to *Asthenotoma* Harris & Burrows 1891. The type of this genus is *Pleurotoma meneghenii* Mayer, by original designation. As figured by Bellardi (1878: 239. *pl. 7, f. 26*), as *Oligotoma tuberculata* (Pusch), this is a high-spired species marked by spiral sculpturing only, and possessing a strong, spiral sutural band. The aperture is short and moderately broad, the anterior canal practically obsolete. It is very different from *Domenginella*.

The outline and general aspect of some of the heterogenous species referred by Hedley (1922: 236–247. *pl. 43, f. 25–27; pl. 44, f. 28–37*) to his genus *Inquisitor* (1918: M79) type, by original designation, *Pleurotoma sterrha* Watson, is similar to *Domenginella*, but there is no evidence of the lirae on the outer lip.

The systematic position of this group is difficult to state. The great similarity in all features save the columella to *Scobinella* Conrad suggests a possible relationship to that group, although the similarity may be due to parallelism in evolutionary development. The presence of true *Scobinella* in the Llajas formation of the Simi Valley lends some support to the concept of close relationship, and *Domenginella* may be a northern development of the *Scobinella* radical. The suggestion that this may be an individual variation of *Scobinella* in which the columellar plications are not present, such as is known in *Borsonella* and other turrid genera,* does not seem to explain the fact that on some fifty specimens examined no trace of these folds is to be noted.

Domenginella claytonensis (Gabb)

PLATE 17, FIGURES 18, 20

Turris claytonensis Gabb (1864) 92. *pl. 18. f. 46* (described, near Clayton).
Pleurotoma claytonensis (Gabb) Stoliczka (1868) 68.
Surcula claytonensis Gabb (1869) 217 (Clayton & Tejon).
Surcula gesteri Dickerson (1916) 434, 452, 499. *pl. 42, f. 4* (described, loc. 672).—Anderson & Hanna (1925) 87 (not at Tejon, from loc. 672 (U. C. Coll.) north of Coalinga).
Turris claytonensis = *Turris gesteri* (Dickerson); Clark (1926) 116 (Coalinga).
Scobinella claytonensis (Gabb); Stewart (1927) 417. *pl. 27, f. 11, 12* (lectotype and synonymy).

* See Grant & Gale (1931) 543, 544, 545, etc.

Hypotype 15775; loc. 672; length 9.3 mm., diameter 3.9 mm.
Hypotype 15776, loc. 672; length 9.3 mm., diameter 3.8 mm.

This is the most abundantly represented turrid species in the Domengine formation. It may be recognized by the double row of nodes on the spire-whorls and by the generally nodose character of the spirals on the body-whorl, as well as by the lirate outer lip and smooth columella.

The basis for Dickerson's record (1916: *pl. 42*, text) of this species from the type Tejon and from the Cowlitz horizon in Washington is not known.

Genus SURCULITES Conrad 1865

GENOTYPE (by monotypy): *Surcula (Surculites) annosa* Conrad. Eocene, Shark River. New Jersey.

Surculites mathewsonii (Gabb)

PLATE 17, FIGURES 8, 19

Fusus mathewsonii Gabb (1864) 83. *pl. 18, f. 33* (described, Martinez).
Fusinus mathewsonii (Gabb); Dickerson (1916) 433, 450 (loc. 672).
Surculites mathewsonii Gabb = *Surcula davidsoni* Cooper; Clark (1926) 116 (Coalinga).
Surculites mathewsonii (Gabb); Stewart (1927) 420, 421. *pl. 26, f. 12, 13, 14* (lectotype and synonymy).—Turner (1938) 70 (variety in the Domengine formation).
Bela clathrata Gabb (1869) 152. *pl. 26, f. 31* (described, Martinez).
Surcula (Surculites) sinuata Gabb; Dickerson (1916) 433, 452 (loc. 672).
? *Pleurotoma decipiens* Cooper (1894) 40. *pl. 2, f. 32* (described, Rose Canyon, San Diego County) Not *Pleurotoma decipiens* Deshayes (1865) 363. *pl. 97, f. 19, 20.*

Hypotype 15777; loc. 672; length (incomplete) 21.7 mm., diameter 18.4 mm.
Hypotype 15778; loc. 672; length (incomplete) 42.0 mm., diameter 29.6 mm.

The variation in the strength of the angulation on the body-whorl below the shoulder is pronounced. The angulated type is the characteristic form, although intergrades between it and the slightly angulated form (hypotype 15778) are not rare. This slightly angulated type was the basis of Dickerson's record (*op. cit.*) of the occurrence of *Surculites sinuata* (Gabb*) at locality 672. This latter species is known only from the Tejon formation. It differs from *S. mathewsonii* in the nature of the spiral ribbing, which lacks secondary riblets, in the higher sutural collar, and in the extreme reduction of the angulation of the body-whorl.

The type of "*Potamides ?*" *davisiana* Cooper is a fragment which appears to be similar to strongly angulated forms in the Lower Llajas and represents a distinct subspecies of *S. mathewsonii*.

* Gabb (1864) 123. *pl. 29, f. 227;* as *Conus sinuatus.*

Genus **CRYPTOCONUS** von Koenen 1867

GENOTYPE (by subsequent designation, Cossmann 1889): *Pleurotoma filosa* Lamarck. Eocene, Paris Basin, France.

Cryptoconus may be distinguished from the superficially similar *Pseudotoma* Bellardi 1875 (type, by monotypy, *P. intorta* Brocchi; Miocene of Italy) and *Megasurcula* Casey 1904 (type, by subsequent designation, Stewart 1927, *Surcula carpenteriana* Gabb; Pliocene to Recent, West Coast of the United States), by its deeper and narrower posterior notch and by the more slender and higher nucleus.

Cryptoconus cooperi (Dickerson)

PLATE 17, FIGURE 17

Drillia cooperi Dickerson (1916) 491. *pl. 40, f. 6 a, b* (described, Marysville Buttes).
Cryptoconus injucundus Hanna (1924) 164.

Hypotype 15780; loc. 4170; length 20.7 mm., diameter 7.2 mm.

Dickerson's type (U. C. Coll. no. 11824) is a fragment lacking most of the body-whorl and all of the aperture and canal, while his "small specimen" (U. C. Coll. no. 11825) is a fragment lacking most of the spire and the outer lip of the aperture. Thus there is no basis for his statement that "the body-whorl and canal are together nearly twice as long as the spire." An examination of additional material indicates that they are more generally of approximately equal length. The "five spiral bands or threads" might be better described as incised lines, there being 3 strongly incised spiral lines immediately below the suture and numerous finer ones over the rest of the whorls. The nucleus is typical of the genus.

"*Pleurotoma (Dolichotoma)*" *cooperi* Arnold (1903: 203. *pl. 7, f. 3.* Pleistocene) has a shallower notch and is apparently a *Megasurcula*, so that Hanna's new name for Dickerson's species, *Cryptoconus injucundus*, is not necessary.

The identification of the Meganos form with this species* is open to question. The spire is higher and the anterior canal much longer, making the whole shell more slender than in the younger Eocene species.

Genus **EXILIA** Conrad 1860

GENOTYPE (by monotypy): *Exilia pergracilis* Conrad. Eocene, Alabama.†

Dall's statement (1918a: 221), "pillar smooth, without plications of any sort," is true only of the more mature specimens. An immature

* Clark & Woodford (1927) 109. *pl. 19, f. 8. 9, 10;* as *Turricula ? cooperi.*
† Dall and subsequent authors have stated that this species is from Texas, but Conrad, in his original description, states "Locality.—Alabama. Dr. Showalter."

specimen in the collections of the University of California from near Oak Hill, Alabama, has 4 spiral lines on the columella, with a suggestion of more present posteriorly. Such spiral markings on the columella in the early stages of development appear to be characteristic of the genus. They are to be observed on *Exilia perkinsiana* (Cooper*) and *Exilia dickersoni* (Weaver†), although in both species the columella is smooth in fully adult specimens. Similar columellar folds were described on *Exilia microptygma* (Gabb‡) and are to be seen in the figure of *Exilia fausta* Anderson & Hanna (1925: 59. *pl. 8, f. 8, 9*).

Exilia cf. perkinsiana (Cooper)

Cf. *Pleurotoma perkinsiana* Cooper (1894) 40. *pl. 2, f. 23, 24* (described, Marysville Buttes).
Cf. *Turris perkinsiana* (Cooper); Dickerson (1913) 277. *pl. 11, f. 7 a, b* (original description, and discussion).—Dickerson (1916) 427 (loc. 1817 and *Siphonalia sutterensis* zone).
Exilia perkinsiana (Cooper); Dickerson (1916) 426, 432, 449 (loc. 1817).

This species was described from the Capay stage at Marysville Buttes. The Coalinga material is too poorly preserved to allow positive identification.

Exilia taliaferroi NEW SPECIES

PLATE 17, FIGURE 21

Holotype 15781; loc. A-978; length 20.4 mm., diameter (crushed) 3.0 mm.

DESCRIPTION.—Shell slender, elongate-fusiform, of 2 or 3 nuclear and 8 post-nuclear whorls which are gently convex in outline, and sculptured by 10 equidistant spiral threads and approximately 14 well-developed, slightly curved axial ribs arranged one above the other on the spire, and becoming obsolete on the base of the body-whorl; spiral ribs crossing the axials, but more strongly developed in the interspaces; 12 strong spirals on the body-whorl posteriorly, with an equal number of finer spirals on the base of the whorl, the anterior extension being marked by numerous very fine threads; suture linear, impressed.

The type of this species is a cast and the entire number of axial ribs is not known, but there do not seem to have been more than fourteen.

COMPARISON.—*E. taliaferroi* is an exceedingly slender species which is remarkable for the manner in which the axial ribs, arranged one above the other, appear to be continuous up the spire. The slender

* Cooper (1894) 40. *pl. 2, f. 23, 24*; as *Pleurotoma perkinsiana*.
† Weaver (1912) 50. *pl. 3, f. 29; pl. 14, f. 124*; as *Fusus dickersoni*.
‡ Gabb (1864) 93, 94. *pl. 28, f. 203*; as *Cordiera microptygma*.

outline and the small number of axial ribs will at once serve to distinguish this from previously described species.

This species is known from a single specimen in the upper zone of the Arroyo Hondo formation.

Named in honor of Dr. N. L. Taliaferro of the Department of Geology, University of California.

Exilia ucalia NEW SPECIES

PLATE 17, FIGURE 11

Fusus diaboli "Gabb"; Anderson (1905) 164 (Avenal sandstones).—Arnold (1909) 14 (region southeast of Big Tar Canyon).—Arnold & Anderson (1910) 72 (region southeast of Big Tar Canyon). Not *Fusus diaboli* Gabb (1864).
Fusinus (*Exilia*) *waringi* "Dickerson"; Clark (1926) 115 (Coalinga).

Holotype 15782; loc. A-976; length (incomplete) 13.6 mm., diameter 4.3 mm.

DESCRIPTION.—Shell small, moderately stout for the genus, the nuclear whorls and anterior portion of canal missing; whorls flat-sided to very gently convex with a slight concavity immediately below the appressed, somewhat channeled suture; ornamentation consisting of sinuous axial ribbing and spiral lines; axial ribs obsolete on the body-whorl, 23 on the penultimate whorl, 19 on the next posterior whorl, and 13 on the preceding turn; spiral sculpturing consisting of 4 fine ribs separated by interspaces as wide as the ribs, immediately below the suture, and 3 strongly developed ribs separated by interspaces slightly wider than the ribs on the anterior portion of the whorl; 4 less strongly developed spirals on the body-whorl below the 3 strong ribs marking the middle surface, separated by interspaces of equal width, the canal marked by moderately strong spirals separated by interspaces three times the width of the ribs with a fine intercalated rib in each; aperture long, narrow, the columella thinly callused with 4 faint columellar folds.

COMPARISON.—The nature of the zones of spiral sculpturing will serve to separate this from other described species. On *E. diaboli* (Gabb*), *E. fausta* Anderson & Hanna, and *E. microptygma* (Gabb) the widely spaced spirals are adjacent to the suture, with the finer spirals on the body of the whorl.

This is the second species of *Exilia* described from the Domengine formation, as *E. diaboli* "from the strata above the coal at Cochran's" is of Domengine age. The specimen representing Hanna's record (M. A. Hanna 1927: 316) of *Exilia* cf. *waringi* Dickerson from the La Jolla formation is not specifically identifiable.

Gabb (1864) 84. *pl. 18, f. 35;* as *Fusus diaboli.*

Family CONIDAE

Genus CONUS Linnaeus 1758

GENOTYPE (by subsequent designation, Children 1823). *Conus marmoreus* Linnaeus. Recent, Indo-Pacific.

Conus marmoreus is the first species on the original list of Linnaeus (1758: 712). Montfort (1810: 407) had cited as the type of *Conus*, *C. fulgurans*, a new name for *C. generalis* Linnaeus, which was not on the original list of species given by Linnaeus in edition 10.

Conus marmoreus, the type of the genus, is characterized most noticeably by the presence of an aperture which is much wider near the base than it is at the shoulder. This feature indicates that neither of the species present in the Domengine fauna belongs to *Conus* (*sensu stricto*). The writer believes that both are probably to be referred to *Leptoconus* Swainson (1840: 312) (type, by subsequent designation, Herrmannsen 1847, *Conus amadis* Martini), although the anal notch is somewhat shallower than is typical in this subgenus.

Conus hornii Gabb umpquaensis Hendon

PLATE 18, FIGURES 2, 3

Conus "*remondi* Gabb;" Stanton (1896) 1027 (New Idria).
Conus hornii Gabb; Dickerson (1916) 432 (in part), 449 (in part) (loc. 672).
Conus hornii var. *umpquaensis* Hendon in Turner (1938) 69. *pl. 15, f. 12.*

Hypotype 15783; loc. A-975; length (incomplete) 9.8 mm., diameter 5.3 mm.
Hypotype 15784; loc. A-1164; length (incomplete) 8.7 mm., diameter 5.2 mm.

This is the most common species of *Conus* in the collections from the Domengine formation. It differs from typical *C. hornii* Gabb (1864: 122. *pl. 29, f. 226*) in having a higher spire and in being on the average smaller than the Tejon specimens. Stanton's record of *C. remondi* Gabb from New Idria is believed to be based upon this species, as it is the only *Conus* in the Vallecitos collections.

Conus caleocius NEW SPECIES

PLATE 18, FIGURES 1, 7

Conus remondii "Gabb;" Clark (1926) 115 (Coalinga).
Conus cf. *remondii* Gabb; Dickerson (1916) 432 (loc. 672).

Holotype 15785; loc. 3310 (Simi Hills, Ventura County); length (incomplete) 10.8 mm., diameter 6.4 mm.
Hypotype 15786; loc. A-1165; length 14.2 mm., diameter 6.7 mm.

DESCRIPTION.—Shell small, biconic, with two smooth, rounded nuclear whorls and six post-nuclear whorls; shoulder of post-nuclear whorls ornamented by well-developed, equidistant nodes (14 on the

body-whorl of the holotype and 11 on the preceding whorl), a second row of smaller nodes immediately below the appressed suture (32 on the body-whorl of the holotype); top of the whorl sculptured by 6 equidistant spiral threads, the first somewhat obscured by the nodes on the shoulder and more prominent in the internode areas, and the fifth less interrupted by the sutural nodes; sides of the whorls sculptured by strong, subequal, rounded spiral cords, 28 on the body-whorl of hypotype 15786; aperture long, narrow, with parallel sides, the anal notch broad and moderately deep.

COMPARISON.—*Conus caleocius* differs from all described West Coast Eocene *Conidae* except *C. warreni* Hendon* in the presence of the strong spiral ornamentation on the body-whorl. *Conus ruckmani* Dickerson (1917: 179. *pl. 31, f, 6 a, b*), from the Greis ranch horizon, Oligocene, of Washington, has fewer, finer, and more widely separated spiral threads, and lacks sculpturing on the shoulders of the whorls. The number of nodes on the shoulder of the new species is intermediate between that on *Conus californianus* (Conrad†) (11 to 12 on the body-whorl) and those forms commonly known as *C. remondii* Gabb from the Tejon, which have 22 to 24 nodes. *C. warreni* Hendon has 20 nodes on the shoulder of the body-whorl, which are smaller and "subdued"; the row of nodes immediately below the suture is also lacking.

ADDITIONAL NOTES.—There appears to be no mistaking the fact that Gabb proposed the name *Conus remondii* as a substitute name for *C. californianus* (Conrad) in the belief that that name had been preoccupied by *C. californicus* Hinds. "The specific name *Californicus* having been used by Hinds for a recent species, I propose the above name in honor of Mr. Remond, who discovered the specimens from which I became acquainted with the species." (Gabb 1864: 122). Since Hinds' name does not invalidate that of Conrad, Gabb's name, being proposed as a substitute name, must be considered to represent an objective synonym of Conrad's name and take the same type specimen. While it is unfortunate that a name as well known as *C. remondii* must be discarded, it is not without practical advantages. The lectotype chosen by Stewart (1927: 414, 415. *pl. 29, f. 15*) to represent this species from the Tejon appears to be specifically distinct from the specimen figured by Gabb, which was probably from Cochran's (of Meganos ? age). The Tejon species has 22 to 24 nodes

* Hendon in Turner (1938) 68. *pl. 15, f. 3, 4.*
† Conrad (1855) 11, as "*Volutatithes*," a typographical error for *Volutilithes*.

on the shoulder of the whorl, lacks spiral ribbing on the shoulder, and has spiral ribs on only the lower portion of the body-whorl. It appears that the name for this species is *C. submoniliferus* Anderson & Hanna (1925: 99, 100. *pl. 8, f. 6*), on the type specimen of which the nodes are subobsolete on the body-whorl. For the Middle Eocene species the name *C. warreni* Hendon appears to be the first available name. This species agrees with the figure given by Gabb in possessing broad spiral ribs separated by narrow interspaces on the body-whorl. It has 20 nodes on the shoulder of the body-whorl, and Gabb's figure indicates 10 on the half of the specimen shown. The specimens figured by Hanna* from San Diego are somewhat intermediate between the two species and probably should have a new subspecific name.

Family CANCELLARIIDAE

Genus BONELLITIA Jousseaume 1887

GENOTYPE: *Bonellitia bonellii* (Bellardi). Tortonian and Plaisancian, Italy.

Bonellitia (?) megapex NEW SPECIES

PLATE 18, FIGURES 4, 5

Cancellaria stantoni Dickerson (1916) 432, 448 (in part, loc. 672) (not 426, 427, 432 (in part), loc. 1817).
Admeta stantoni "Dickerson"; Clark (1926) 115 (Coalinga).

Holotype 15889; loc. 672; length 5.0 mm., diameter 2.9 mm.
Paratype 15890; loc. 672; length 4.6 mm., diameter 2.8 mm.

DESCRIPTION.—Shell small, moderately stout, of 6 whorls, the first three smooth, flat-topped, enlarging rapidly to form a large and prominent nucleus, the fourth convex, biangulated by 2 prominent spirals continuing as the primary spirals on the later whorls; approximately three fourths of the circumference of the fourth whorl with this spiral sculpturing only, the last fourth with axial ribbing from suture to suture at its inception; the fifth (penultimate) whorl with 11 axials, the body-whorl with 14; axial ribs sometimes swollen to form varices, but usually of normal strength and noded where crossed by the primary spiral; anterior primary spiral approximately one half the distance between the angulation and the somewhat irregular linear suture; interspaces separating the primaries from each other and from the sutures marked by a secondary rib; a third primary spiral on the body-whorl, and between each of the primary and secondary ribs a tertiary riblet; the base of the whorl sculptured by

* M. A. Hanna (1927) *pl. 56, f. 4, 5, 15, 16*; as *C. remondi*.

secondary and tertiary spirals, the axials being obsolete; aperture broadly ovate, the interior of the outer lip marked by 6 denticulations opposite the varices, simple in the areas between the varices, the inner lip thinly callused; columella with 3 prominent plications progressively stronger posteriorly; anterior canal short, slightly emarginate.

COMPARISON.—*Bonellitia* (?) *megapex* differs from "*Cancellaria*" *stantoni* Dickerson (1913: 282. *pl. 12, f. 2 a, b;* described, Marysville Buttes), with which it has been confused, in the nature of the spiral sculpturing, in which 4 or 5 spirals appear simultaneously, rather than 2; on the penultimate whorl there are 3 primary and no secondary ribs between the posterior pair, although a secondary is present on the shoulder, separated from the posterior primary by a fine tertiary riblet; on the body-whorl there are 5 primary threads with secondary and tertiary riblets in the interspaces. The axial ribs are slightly more numerous. "*Cancellaria*" *bournei* M. A. Hanna (1927: 323. *pl. 55, f. 1, 3, 4, 6;* described, La Jolla formation) shows 7 spirals at the inception of the sculpturing, with secondary ribbing rare, and tertiary ribbing absent on the body-whorl.

The very large, swollen naticoid nucleus which marks these three species does not appear to be typical of *Bonellitia* (*sensu stricto*) and further study with adequate comparative material will probably result in their generic segregation.

Suborder RACHIGLOSSA

Family OLIVIDAE

Genus OLIVELLA Swainson 1835

GENOTYPE (by subsequent designation, Dall 1909): *Olivella purpurata* Swainson = *O. dama* Mawe. Recent, Pacific Coast of Mexico.

Olivella cf. mathewsonii Gabb

Cf. *Olivella mathewsonii* Gabb (1869) 220 (Griswold's).—Dickerson (1916) 451 (Coalinga District).

Family ANCILLIDAE

Genus ANCILLA Lamarck 1799

GENOTYPE (by monotypy, Lamarck 1801) · *Ancilla cinnamomea* Lamarck. Recent, Red Sea, Persian Gulf, and Zanzibar.

In the original description of the genus Lamarck cites, apparently as an example, "Voluta . . . Martin, conch. 2, p. 359, t. 65, f. 722–724." Woodring (1928: 234) has identified this as "*Voluta* (*basi*

constricti etc.) Martini (= *Voluta ampla* Gmelin, *Ancillaria candida* Lamarck)." The writer is of the opinion that since no species was mentioned by name this must be considered to represent a genus without species. In 1801, Lamarck cited as the example of the genus *Ancilla cinnamomea* Lamarck, which becomes the monotype species.

Sparella Gray 1857, type (by original designation) *A. ventricosa* Lamarck, is synonymous, as (*fide* Tryon*) that species is synonymous with *A. cinnamomea.*

Subgenus SPIRANCILLA Vokes 1934

TYPE SPECIES (by original designation): *Ancilla buccinoides* Lamarck. Eocene, Paris Basin, France.

Ancilla buccinoides has been cited as the type of *Ancilla* Lamarck by Montfort (1810: 383) and by Cossmann (1899: 58), and appears to have been so considered by a number of other workers. As a result of this erroneous concept there appears to be no name available for the group of species including *Ancilla buccinoides* Lamarck of the Paris Basin and *A. gabbi* Cossmann of the California Eocene. In Cossmann's arrangement, "*Ancillaria*" *tankervillei* Swainson, a Recent species, is considered to belong to the same group as *A. buccinoides* (*Ancilla sensu stricto*). This species, which is the type of *Amalda* H. & A. Adams and of *Sandella* Gray, has a prominent tooth-like projection on the anterior portion of the outer lip and seems to represent a distinct species-group.

The reader is referred to Cossmann's discussion of "*Ancilla* s. restr." for a diagnosis of this subgenus.

Ancilla (Spirancilla) gabbi Cossmann

PLATE 18, FIGURES 6, 10

Ancillaria elongata Gabb (1864) 100. *pl. 18, f. 54* (described, San Diego) —Dickerson (1916) 426, 427, 432, 448 (loc. 1817).—Clark in M. A. Hanna (1927) 260 (Coalinga).
Ancellaria elongata Gabb; Anderson (1905) 164 (Avenal sandstones).
Cancellaria elongata Gabb, Anderson in Arnold (1909) 14 (southeast of Big Tar Canyon).—Anderson in Arnold & Anderson (1910) 72 (southeast of Big Tar Canyon).
Ancilla elongata Gabb; Clark (1926) 115 (Coalinga). Not *Ancillaria elongata* Michelotti 1847; nor *Ancillaria elongata* Gray (1847a) 357. *pl. 1, f. 5.*
Ancilla gabbi Cossmann (1899) 60, footnote. (new name).

Hypotype 15787 loc. 672; length 14 6 mm , diameter 5.7 mm.
Hypotype 15788; loc. 672; length 10.6 mm., diameter 4.4 mm.

Genus CORALLIOPHILA H. & A. Adams 1853

GENOTYPE (by subsequent designation, Cox 1927): *Purpura violacea* Kiener. Recent, Indo-Pacific.

* Tryon (1883) 93 *pl. 37, f 2–17.*

Coralliophila dubia (Merriam & Turner)

PLATE 18, FIGURES 8, 9

Lacinia ? dubia Merriam & Turner (1937) 103. *pl. 5, f. 14. 15. 16, 17.*

Topotype 15801; loc. A-1314; length 16.4 mm., diameter 14.6 mm.

This species resembles closely, both in the nature of the rather sinuous growth-line and the development of a strong callus on the inner lip and the posterior portion of the aperture, specimens of *Coralliophila porphyroleuca* (Crosse) from the Paumoto Islands, in the invertebrate collections of the Museum of Paleontology. *C. violacea,* the genotype does not show the same tendency to develop a heavy apertural callus, has a series of longitudinal denticulations on the inner edge of the outer lip, and the growth-line is straight. *Expleritoma prima,* as figured by Aldrich (1886: *pl. 5, f. 1*), possesses a higher spire and apparently has a tendency to resorb the inner lip, although Aldrich mentions a young shell in which the spire is flattened.

Melapium lineatum (Lamarck), the monotype species of *Melapium* H. & A. Adams, possesses a similar type of apertural callus but has a large papillary spire.

Two specimens from the Vallecitos, locality A-1017, occur in the collections.

Family MARGINELLIDAE

Genus MARGINELLA Lamarck 1799

GENOTYPE (by monotypy): *Voluta glabella* Linnaeus. Recent, West Africa.

Subgenus LEPTEGOUANA Woodring 1928

TYPE SPECIES (by original designation): *Voluta guttata* Dillwyn. Recent, West Indies and Florida.

The species here questionably referred to this subgenus differs from the typical species in possessing a faintly developed fifth columellar fold immediately posterior to the four strongly developed folds which are present in *Leptegouana* (*sensu stricto*). It appears, however, to be more closely related to this group than to any of the other described *Marginella* subgenera.

Marginella (Leptegouana ?) hulini NEW SPECIES

PLATE 18, FIGURES 12, 13, 14

Holotype 15891; loc. A-1016; length 4.0 mm., diameter 2.6 mm.
Paratype 15892; loc. A-1016; length 3.4 mm., diameter 1.9 mm.
Paratype 15893; loc. A-1014; length 3.6 mm., diameter (incomplete) 1.8 mm.

DESCRIPTION.—Shell small, moderately stout, smooth; spire low; aperture long, narrow, emarginate at the base; outer lip thick, cal-

lused, finely denticulate within; columella with 4 strong folds and a faintly developed fifth fold immediately posterior to the fourth; preserved color-pattern showing as exceedingly zigzag light lines on a dark background.

COMPARISON.—*M. hulini* most nearly resembles *M. adumbrata* Anderson & Hanna* but differs in possessing a lower spire and in being stouter in proportion to the length. The color-pattern, which is of light lines on a dark background rather than the reverse, is much more complicated. *M. multifilosa* Anderson & Hanna† is shorter and stouter, with 6 plaits on the columella.

Named for Professor C. D. Hulin of the Department of Geology, University of California, in appreciation of his assistance in solving perplexing stratigraphic problems.

Family MITRIDAE

Genus MITRA Martyn 1784

GENOTYPE (by subsequent designation, Dall 1905): *Mitra tessellata* Martyn. Recent, Indo-Pacific.

Mitra simplicissima Cooper

Mitra simplicissima Cooper (1894) 45. *pl. 3, f. 41* (described, San Diego).—Dickerson (1916) 426, 427, 450 (loc. 1817).
Mitra simplicimma Gabb; Clark (1926) 116 (Coalinga).

The Coalinga specimens are uniformly smaller than those from the Llajas formation, which in turn are smaller than the San Diego specimens. This difference in size is possibly to be correlated with temperature factors.

The type species of the genus *Mitra* is a high-spired shell, with prominent spiral and crude axial ribs, a broad aperture, a short anterior canal, and a wide siphonal notch. *Conomitra* Conrad 1865 (type *Mitra fusoides* Lea), as used by Cossmann,‡ would include *M. simplicissima*, but the type species does not possess the long narrow aperture and well-developed anterior canal. *Plioptygma* Conrad 1862 (type *Mitra carolinensis* Conrad) has a comparable aperture, but the spire is much shorter and the whole shell stouter.

Genus MITROMORPHA "Adams" Carpenter 1865

GENOTYPE (by monotypy): *Daphnella ? filosa* Carpenter. Recent, California and Mexico.

* Anderson & Hanna (1925) 78. *pl. 9, f. 2; pl. 15, f. 6* (described, Tejon).
† Anderson & Hanna (1925) 79. *pl. 7, f. 2, 3* (described, Tejon).
‡ Cossmann (1899) 172.

Mitromorpha (?) parsonsi Dickerson

"*Mitramorpha*" *parsonsi* Dickerson (1916) 433, 450, 495. *pl. 38, f. 11* (described, loc. 672).—Clark (1926) 116 (Coalinga).—Woodring (1928) 249 (not a *Mitromorpha*).
Mitromorpha parsonsi Cossmann (1916) 110.
"*Mitramorpha parsoni*" Dickerson; Anderson & Hanna (1925) 95 ("apparently a *Mangilia*").

The type of this species apparently has been lost, and it is represented in the collections only by a fragment from the typical locality. Until better material is obtained it is not practicable to attempt to make any generic determinations; as stated by Woodring, this species is not a *Mitromorpha*. It is rather similar to *Vexillum* "Bolten" Roeding, type (by subsequent designation, Woodring 1928) *Vexillum plicatum* "Bolten" Roeding (= *Voluta plicaria* Linnaeus), but has a larger number of columellar plications and lacks the lirations on the interior of the outer lip. It will probably take a new generic name, together with "*Mitramorpha*" *howei* M. A. Hanna* from the La Jolla formation, which has a greater number of columellar plications (eight) than has "*M.*" *parsonsi* (six).

Genus **UROMITRA** Bellardi 1887

GENOTYPE (by subsequent designation, Cossmann 1899): *Voluta cupressina* Brocchi. Miocene-Pliocene, Italy.

Conrad† proposed this name as a subgenus of *Mitra*, but Cossmann‡, although stating that the aperture is "depourvue de gouttière posterieure," considers it to represent a subgenus of *Turricula*. The absence of the posterior sinus would, in the writer's opinion, make the reference of the group to the *Mitridae* more satisfactory.

Uromitra (?) cretacea (Gabb)

PLATE 18, FIGURE 19

Mitra cretacea Gabb (1864) 103. *pl. 28, f. 215* (described, Martinez).—Gabb (1869) 158, 221 (additional description).—Stewart (1927) 406. *pl. 27, f. 9, 10* (holotype and synonymy).

Hypotype 15894; loc. A-1164; length (incomplete) 14.1 mm., diameter 6.6 mm.

The single specimen in the collections from the Domengine formation is more slender than the figures of the holotype; the spire is higher and the nodes on the shoulder are broader and less distinctly developed. However, few specimens representing this species are known and until the range of variation is determined it is thought best to refer the specimen to Gabb's species.

* M. A. Hanna (1927) 322. *pl. 53, f. 6 and 8.*
† Conrad (1865) 25.
‡ Cossmann (1899) 166.

The aperture is approximately as long as the spire, the anterior canal long and straight with 3 strong columellar plications and a weaker fold anteriorly.

The spire and general outline of this species is very similar to that of many of the *Turridae*, but it lacks all trace of a posterior sinus.

Family VOLUTIDAE

Genus VOLUTA Linnaeus 1758

GENOTYPE (by subsequent designation, Montfort 1810): *Voluta musica* Linnaeus. Recent, West Indies (*fide* Tryon).

The Eocene species which have been referred to *Voluta* are not typical, and appear to need a new subgeneric name. *Voluta musica* has 12 or more columellar folds which become progressively heavier and more pronounced anteriorly, and are present along the full length of the aperture. The Eocene species possess but 4 folds, which become progressively stronger posteriorly and do not appear on the posterior third of the columellar lip.

The statement by Grant & Gale* that *Voluta* Linnaeus has 4 columellar plications is apparently based upon Eocene material.

Voluta (?) eomagna NEW SPECIES

PLATE 18, FIGURE 18

Lyria sp. Turner (1938) 73 (Domengine, north of Coalinga).

Holotype 15789; loc. A-973; length (incomplete) 70.0 mm., diameter 39.5 mm.

DESCRIPTION.—Shell large, heavy, of 2+ whorls, the nucleus and early post-nuclear whorls missing; width of body-whorl approximately two thirds the length, smooth, the shoulder marked by 8 spinose nodes (9 on the penultimate whorl); above the shoulder nodes a strongly concave collar sloping to the linear suture; aperture long, moderately narrow, the outer lip simple, the inner lip thinly callused with 4 columellar plications anteriorly, these progressively stronger posteriorly; siphonal fasciole large; anterior canal short, recurved.

COMPARISON.—*Voluta* (?) *eomagna* differs from "*Lyria*" *coquillensis* Turner† in possessing 8 spinose nodes, which are rounded, rather than the 6 elongate nodes of the Oregon species; the sutural collar is wider, with the suture less distinctly appressed, and the siphonal fasciole is more heavily developed and less oblique.

* Grant & Gale (1931) 633.

† Turner (1938) 73. *pl. 18, f. 12.*

Turner seems to have overestimated the significance of the small nucleus in referring his species to *Lyria* Gray. According to Dall, the size of the nucleus appears to be a function of the amount of nourishment the individual receives while in the egg-case, and the same egg-case seems to give rise to individuals with either large or small nuclei.

Only two specimens representing this species are known: the holotype and a specimen from the La Jolla formation in the Sternberg Collection at the Peabody Museum of Natural History, Yale University.

Genus LYRIA Gray 1847

GENOTYPE (by monotypy): *Voluta nucleus* Lamarck. Recent, North Australia (Reeve).

Lyria andersoni Waring

PLATE 18, FIGURES 22, 24

Cancellaria irelaniana "Cooper"; Arnold (1909) 13, 52. *pl. 4, f. 22* (S. W. of Domengine's Ranch).—Arnold & Anderson (1910) 71. *pl. 26, f. 22* (S. W. of Domengine's Ranch).—Dickerson (1913) 264, 282 (Coalinga).—Dickerson (1916) 449 (? from Coalinga).

Lyria andersoni Waring (1917) 97. *pl. 15, f. 12* (described, Simi Valley, "Probably Arnold's *Cancellaria irelaniana* belongs to this genus").—Clark (1921) 159 ("Meganos," north of Coalinga).—Clark (1926) 115 (Coalinga).

Hypotype 15790; loc. 3958; length 38.3 mm., diameter of body whorl 17.5 mm.

Four specimens representing this species occur in the collections. All are larger than any from the Simi Valley Eocene, but agree in all other characters with the topotype material. There are 5 plaits on the columella.

Family FASCIOLARIIDAE

Genus FUSINUS Rafinesque 1815

GENOTYPE (by monotypy, Lamarck 1799): *Murex colus* Linnaeus. Recent, Indo-Pacific.

The generic name *Fusinus* was proposed as a substitute name for *Fusus* Lamarck. The following species is tentatively assigned to this genus, although lacking the nuclear characters which Grabau's study* has made essential in the classification of this group.

The reference by Etherington† to "*Fusus*" *colus* as a species from the Eocene of the Paris Basin is an obvious error, although according to Grabau (*op. cit.*) the only Eocene species which can be referred to *Fusinus* (*sensu stricto*) are to be found there.

* Grabau (1904).

† Etherington (1931) 105.

Fusinus ucalius NEW SPECIES

PLATE 18, FIGURE 15

Holotype 15477; loc. A-816; length (incomplete) 39.7 mm., diameter 13.3 mm.

DESCRIPTION.—Shell of medium size, moderately slender, of 5 whorls, the nuclear and early post-nuclear whorls missing; whorls strongly convex, sculptured by swollen axial ribs and strong spiral lines, the axials most strongly developed just anterior to the center of the spire-whorls and forming an angulation marked by a strong spiral, with 2 similarly strong spirals anterior forming subangulations where crossing the axials; spirals posterior to the angulation less strongly developed, 2 primary spirals alternating with 3 secondary spirals; axials on the body-whorl probably 8, extending to the base of the whorl but not present on the canal, the anterior spirals all of primary strength but subobsolete, and showing secondary ribbing on the canal; suture appressed, linear; aperture not seen; anterior canal long, straight.

COMPARISON.—*Fusinus ucalius* may be distinguished from *F. voetus* M. A. Hanna* and *F. meganosensis* Clark & Woodford† by the subobsolete nature of the axials on the posterior portion of the spire-whorls; these ribs on the previously described species extend from suture to suture. *Fusinus teglandae* M. A. Hanna‡ lacks prominent axial ribbing on the later whorls. *Fusinus merriami* Dickerson§ has a strongly nodose central carina and appears to be a *Fulgurofusus*.

Pleurotoma guibersoni Arnold¶ may represent this species. The type is poorly preserved and lacks the anterior canal, and if conspecific represents a very immature individual; until further evidence is available it has seemed best to separate the present form from Arnold's species.

Genus **FALSIFUSUS** Grabau 1904

GENOTYPE (by original designation): *Fusus meyeri* Aldrich (not Dunker) = *Fusus ottonis* Aldrich. Eocene, Midway, Alabama.

This generic name was proposed by Grabau for "shells with a *Fusus* form and *Pleurotoma* protoconch."

* M. A. Hanna (1927) 316. *pl. 51, f. 1, 2, 4.*
† Clark & Woodford (1927) 111. *pl. 19, f. 13.*
‡ M. A. Hanna (1927) 315. *pl. 51, f. 9.*
§ Dickerson (1916) 493. *pl. 40, f. 2 a, b.*
¶ Arnold (1909) 14, 54. *pl. 4, f. 20.*

Falsifusus marysvillensis (Merriam & Turner)

PLATE 18, FIGURE 11

Turris suturalis (Cooper); Dickerson (1913) 276. *pl. 11, f. 6 a, b* (Marysville Buttes).—Dickerson (1916) 427, 434, 453 (loc. 1817). Not *Mangilia suturalis* Cooper (1894) 41 (described, Marysville Buttes).
Fusinus marysvillensis Merriam & Turner (1937) 102. *pl. 5, f. 1, 2* (described, Marsyville Buttes), 100 (Lillis Ranch).

Hypotype 15791; loc. 1817; length 24.8 mm., diameter (slightly crushed) 9.3 mm.

Well-preserved nuclei of this species exhibit the characters indicated by Grabau* as being typical of *Falsifusus*.

Family HARPIDAE

Genus HARPA (Bolten) Roeding 1798

GENOTYPE (by tautonomy): *Harpa nobilis* Bolten = *Buccinum harpa* Linnaeus. Recent, Philippine Islands (*fide* Reeve, Conch. Icon. 1).

Subgenus EOCITHARA Fischer 1883

TYPE SPECIES (by monotypy): *Harpa mutica* Lamarck. Eocene, Paris Basin, France.

Harpa (Eocithara) clarki Vokes

PLATE 18, FIGURE 26

Harpa (Eocithara) clarki Vokes (1937) 11. *pl. 2, f. 5, 7.*

Holotype 15792; loc. A-1165; length 26.4 mm., diameter 14.6 mm.

Family BUCCINIDAE

Genus UMPQUAIA Turner 1938

GENOTYPE (by original designation): *Umpquaia oregonensis* Turner.† Eocene, Oregon.

This genus is characterized by its robust form, short heavy columella, tabulate flanged later whorls, and a sinuous growth-line below the flange.

The Domengine species referred to this genus is also very similar in many characteristics to the genus *Bruclarkia* Trask in Stewart 1927,‡ and it is quite probable that that genus has developed from the Eocene form.

Umpquaia flangella NEW SPECIES

PLATE 18, FIGURES 16, 17, 20, 21

Holotype 15793; loc. A-1020; length (incomplete) 32.0 mm., diameter 17.2 mm.
Paratype 15794; loc. A-1154; length (incomplete) 23.2 mm., diameter 14.3 mm.
Paratype 15795; loc. A-1154; length 14.4 mm., diameter 8.7 mm.

---

* Grabau (1904) 80. *pl. 17, f. 9.*
† PLATE 18, FIGURE 30 (= Turner 1938: *pl. 16, f. 20, 21*).
‡ Trask in Stewart (1927) 397–399. Type species, *Clavella gravida* Gabb.

DESCRIPTION.—Shell of medium size; length of spire variable, generally half the height; suture impressed; whorls shouldered, sculptured by 10 to 12 swollen axial ribs and numerous spiral threads; axial ribs most strongly developed on the earlier post-nuclear whorls, becoming confined to the shoulder of the body-whorl; body-whorl marked by a strong spiral cord, the spiral threads rounded and separated by interspaces of equal width in which fine inter-ribs may be present; growth-line sinuous, with a broad, shallow notch on the shoulder of the whorl and a forward projection near the middle of the whorl; an area on the surface of the body-whorl in which the spiral ribbing is not present corresponding to the area in which the growth-lines project forward; later whorls developing a broad, thin flange projecting above the suture which may extend beyond the shoulder of the whorl and is ornamented only by lines of growth; aperture broadly angulate posteriorly, short, slightly recurved; inner lip callused, especially posteriorly; fasciole well developed, smooth except for lines of growth.

COMPARISON.—*U. flangella* differs from *U. oregonensis*, the genotype, in possessing axial ribbing and a well defined shoulder on the whorl; the posterior portion of the aperture on the Domengine species is broadly angulate, while in the Oregon form it is broad and flat, a reflection of the tabulate later whorls of that species.

Genus PSEUDOLIVA Swainson 1840

GENOTYPE (by monotypy): *Pseudoliva plumbea* (Chemnitz). Recent, West Coast of Africa.

Pseudoliva lineata Gabb

PLATE 18, FIGURE 23

Pseudoliva lineata Gabb (1864) 99. *pl. 18, f. 52* (described, Martinez).—Stewart (1927) 400. *pl. 28, f. 14, a* (synonymy and lectotype).

Hypotype 15796; loc. 4169; length 28.2 mm., diameter 21.0 mm.

Specimens from the Domengine formation referred to this species possess a spire that is lower than that on the lectotype as figured by Stewart. Specimens from the Llajas formation (Simi Valley) show a spire that is higher than that of the lectotype, and this character seems to be very variable.

This species is rare in the collections from the Reef Ridge section and absent from other areas in the Coalinga collections.

Genus CRYPTOCHORDA Mörch 1858

GENOTYPE (by original designation): *Buccinum stromboides* Herman. Eocene, Paris Basin, France.

Cryptochorda californica (Cooper)

Ancilla (Oliverato) californica Cooper (1894) 43. *pl. 1, f. 6, 7, 8, 9, 10, 11* (described, Marysville Buttes).
Caricella stormsiana Dickerson (1913) 287. *pl. 13, f. 3 a, b* (described, Marysville Buttes).

The specimens representing this species in the Domengine formation are slightly less heavily calloused and have a somewhat higher spire than the forms from the Capay stage at the Marysville Buttes. A single individual from the upper beds of the Arroyo Hondo formation near Domengine Creek is similar to the Domengine specimens.

Genus JANIOPSIS Rovereto 1899

GENOTYPE (by subsequent designation): *Murex angulosus* Brocchi. Miocene, Italy.

Janiopsis (?) kreyenhageni (Arnold)

PLATE 18, FIGURES 25, 27, 28, 29

Tritonidea kreyenhageni Arnold (1909) 14, 51. *pl. 4, f. 10* (described, San Joaquin Coal Mine).—Arnold & Anderson (1910) 71. *pl. 26, f. 10* (San Joaquin Coal Mine).

Topotype 15895; loc. 7155; length (incomplete) 15.9 mm., diameter 8.8 mm.
Topotype 15896; loc. 7155; length (incomplete) 12.3 mm., diameter 8.6 mm.
Topotype 15897; loc. 7155; length 5.9 mm., diameter 3.4 mm.
Topotype 15898; loc. 7155; length (incomplete) 11.7 mm., diameter 6.8 mm.

The siphonal fasciole of this species appears to be slightly more prominent and the 3 columellar folds somewhat more obsolete than is characteristic of the genotype. *Endopachychilus* Cossmann 1889, type (by original designation) *Purpura crassilabrum* Deshayes, appears to lack the columellar folds and to have a thickened outer lip. *Engoniophos* Woodring 1928, type (by original designation) *Phos erectus* Guppy, possesses a stromboid notch on the outer lip which, although internally lirate, is not dentate.

Family ALECTRIONIDAE

Genus MOLOPOPHORUS Gabb 1869

GENOTYPE (by monotypy): *Bullia (Molopophorus) striata* Gabb. Tejon formation, Eocene, California.

Cossmann* questionably places this genus in synonymy with *Cominella* Gray 1857, type (*fide* Cossmann) *Buccinum porcatum* Gmelin. This species is characterized by the development of strong spiral sculpturing and absence of axial ribs; the siphonal fasciole is smooth except for lines of growth; and the posterior siphonal canal is strongly developed. In *Molopophorus* both spiral and axial ribbing is present, and they are of equal strength or the axial ribbing is predominant;

* Cossmann (1901) 149.

the siphonal fasciole bears 2 (or 3) strong folds, and the posterior siphonal canal, while present, is not well developed.

Cossmann seems to have greatly misinterpreted the genus *Cominella.* Judging solely from the figures given by Cossmann & Pissarro,* none of the species referred to that genus from the Eocene of the Paris Basin appear to be correctly referable to *Cominella* (*sensu stricto*). "*Cominella*" *deserta* (Solander) is probably to be referred to the group which has been called *Siphonalia* by the West Coast paleontologists; "*Cominella*" *ovata* (Deshayes) and "*Cominella*" *acies* (Watelet) appear to belong in the genus *Molopophorus;* "*Cominella*" *lata* (Deshayes) has a siphonal fasciole very similar to that of *Molopophorus,* but possesses only spiral sculpture; "*Cominella*" *bicoronata* (Melleville) seems to possess columellar plications, and may be referable to some subgeneric group of *Phos;* "*Cominella*" *auversiensis* (Deshayes) appears to be the species most similar to *Cominella,* but as figured there is a peculiar fold or plication on the anterior portion of the columella which is not typical of that genus. The figures of "*Cominella*" *desori* (Deshayes) are too poor to permit adequate comparisons, but the species appears to have well-developed folds upon the siphonal fasciole, and a smooth shell.

The California species of the genus *Molopophorus* are in need of revision. There are two or three distinct types of nuclear whorls present on species referred to this genus, and it is doubtful if all can be considered congeneric.

The Coalinga specimens referable to this genus fall into three groups which are here treated as distinct species. It is not impossible that all are representative of one exceedingly variable species in which the range of variation is greater than has been observed in any well-known species referable to this genus. The geographic range of these groups, however, suggests that they are distinct species. *M. antiquatus* (Gabb) is known only from the Reef Ridge section and the east end of the Vallecitos; *M. cretaceus* (Gabb) occurs at loc. 672 and in the western portion of the Vallecitos; while *M. aequicostatus* is known only from locality 672.

Molopophorus cretaceus (Gabb)

PLATE 19, FIGURE 4

Nassa cretacea Gabb (1864) 97 (described, Martinez).—Gabb (1869) 219 (ten miles W. of Griswold's).—Dickerson (1916) 433, 451 (loc. 672).

Molopophorus cretaceus (Gabb); Stewart (1927) 391. *pl. 28, f. 9* (lectotype and synonymy).

Hypotype 15937; loc. A-1366; length (incomplete) 10.8 mm., diameter 6.5 mm.

* Cossmann & Pissarro (1911) *pl. 37*, sp. 178–1 to 178–7.

The specimen figured is from Gabb's collections "10 miles W. of Griswold's." Only three specimens which agree with Stewart's description of the lectotype are in the collection. They have from 19 to 25 axial ribs, the sutural collar is marked by 2 strong spiral ribs, and there are approximately 21 other spiral threads on the body-whorl, the anterior 4 or 5 of which are more strongly developed than the rest. Two of these specimens are in the Gabb collection, the other from loc. 672.

This species was described from "Bulls Head Point," Martinez, in strata which are correlated with the Domengine formation.

"*Nassa*" *packardi* Weaver* from the Cowlitz formation of Washington appears to be similar to this species. It is described as possessing 25 axial ribs; 16 spiral ribs and a sutural collar appear to be present, but the poor figure does not permit any definite conclusions.

Molopophorus antiquatus (Gabb)

PLATE 19, FIGURES 1, 2, 3

Nassa antiquata Gabb (1864) 97. *pl. 18, f. 50* (described, Martinez).—Dickerson (1916) 433, 451 (loc. 672).
Molopophorus antiquatus (Gabb); Stewart (1927) 390. *pl. 28, f. 4* (holotype and synonymy).

Hypotype 15938; loc. A-819; length (incomplete) 16.5 mm., diameter 9.6 mm.
Hypotype 15939; loc. A-819; length 8.8 mm., diameter 5.0 mm.
Hypotype 15940; loc. A-818; length (incomplete) 11.6 mm., diameter 8.7 mm.

This species is represented by a number of specimens from the Reef Ridge section, and a few from the eastern end of the Vallecitos syncline. Dickerson's specimen, upon which the record of its occurrence at loc. 672 is based, is incomplete and the identification is not certain.

Stewart has suggested that this may be a variant of *M. cretaceus* (Gabb), and the early whorls of some specimens suggest that it may represent an adult form of that species. The evidence consists of a similar number of axial ribs on the whorl (fewer on *M. cretaceus* than on adult *M. antiquatus*). Hypotype 15939, however, represents a form definitely more immature than specimens of *M. cretaceus*, and possesses characters typical of *M. antiquatus*. This, together with the nature of the occurrence of the two forms, which are not in association, unless Dickerson's specimen from loc. 672 is *M. antiquatus*, does not confirm the suggested relationship for these species and they are here considered to be distinct.

* Weaver (1912) 43. *pl. 3, f.* ,

Molopophorus aequicostatus NEW SPECIES

PLATE 19, FIGURE 5

? *Nassa packardi* Weaver; Dickerson (1916) 433, 451 (loc. 672).

Holotype 15941; loc. 672; length 10.0 mm., diameter 6.5 mm.

DESCRIPTION.—Shell moderately small, heavy, of 2 nuclear and 4 post-nuclear whorls; nucleus rather large, bulbous, naticoid; first post-nuclear whorl décolleté; second post-nuclear whorl with 2 strong spiral threads and 14 axial ribs, the posterior spiral marking the sutural collar, the anterior spiral the shoulder of the whorl, and separated from the posterior by a concave area, the crossing of the 2 types of ribbing marked by small nodes; the third whorl with 19 axial ribs and 6 spiral threads, 2 minor threads having appeared in the concave area between the anterior and posterior threads of the second whorl, and 2 strong threads being present below the anterior thread on the whorl; body-whorl with 31 axial ribs, and 17 spiral ribs, noded where they cross the axials, the sutural rib slightly more prominent than the rest, and the 2 immediately below it the least developed; spiral ribs broad and rounded, separated by interspaces of lesser width except the 2 ribs on the shoulder of the whorl, these being separated by interspaces approximately twice as wide as the ribs; axial ribs broadly rounded and separated by round-bottomed interspaces of slightly greater width; aperture elliptic, narrow; outer lip thick; inner lip heavily calloused; canal short, reflexed anteriorly; siphonal fasciole with 2 strongly developed plications.

COMPARISON.—*M. aequicostatus* may be distingushed from the described species of this genus by the possession of spiral ribbing which is as strongly developed as the axial ribbing, and which is noded where the two types of ribs meet. *M. cretaceus* (Gabb) has axial ribbing which, especially on the spire, is much more strongly developed than the spiral ribs; the axial ribbing is narrower and more widely separated, and tends to become obsolete on the base of the whorl; the spiral ribs are finer and much more numerous (23 on the body-whorl of the specimen figured). The ribbing in *M. antiquatus* (Gabb) is finer in every detail and the ribs are more numerous.

Family MURICIDAE

Genus MURICOPSIS Bucquoy & Dautzenberg 1882

GENOTYPE (by monotypy): *Murex blainvillei* Payrandeau. Recent, Mediterranean Sea.

The following species has been referred to this genus mainly for want of a better systematic position. Specimens of *Murex blainvillei*

are not available, but that species has been considered by Tryon* to be only varietally distinct from *Murex cristatus* Brocchi. Specimens from Naples labelled as that species in the invertebrate collections of the Museum of Paleontology of the University of California appear to have a somewhat longer canal which is less sharply recurved than is observable on the Eocene specimens. The partial roofing of the canal by the callus of the basal portion of the inner lip has not been seen on the fossil forms, although some suggestions that it may have been present are observed.

Muricopsis (?) whitneyi (Gabb) VARIETY

PLATE 19, FIGURES 7, 12

Tritonium whitneyi Gabb (1864) 96. *pl. 28, f. 210, a* (described, Tejon). Not *Nyctilochus* cf. *whitneyi* (Gabb); Dickerson (1916) 427, 451 (loc. 1817).
Murex whitneyi (Gabb); Stewart (1927) 387. *pl. 30, f. 10* (lectotype and synonymy).
Murex beali Anderson & Hanna (1925) 50. *pl. 13, f. 16* (described, Tejon).

Hypotype 15797; loc. A-1020; length (incomplete) 14.6 mm., diameter 9.2 mm.
Hypotype 15798; loc. A-1020; length (incomplete) 14.7 mm., diameter 11.4 mm.

The Domengine specimens differ from the typical Tejon forms in possessing, on the average, one more axial "varix" on the body-whorl. The observed number of varices may be tabulated:

No. of varices on body-whorl:	6,	7,	8,	9.
Tejon specimens..........	5,	5,	–,	–.
Domengine specimens......	–,	8,	15,	4.

There is also a tendency observable on the Domengine specimens to have the lower row of nodes slightly further below the periphery than is characteristic of the Tejon specimens.

Family MURICIDAE ?

Genus PSEUDOPERISSOLAX Clark 1918

GENOTYPE (by original designation): *Perissolax blakei* (Conrad) = *Busycon ? blakei* Conrad. Eocene, Tejon, California.

Stewart† has recently compared *Pseudoperissolax blakei* (Conrad), *Perissolax trivolva* (Gabb), the type (by subsequent designation, Whitfield 1892) of *Perissolax* Gabb 1861‡, with "*Perissolax*" *eocensis* (Aldrich§) and, concluding that both of the first named species are

* Tryon (1880) 108.
† Stewart (1930) 41, 42.
‡ Gabb (1861) 122.
§ Aldrich (1895) 10. *pl. 3, f. 7, 7 a;* as *Fulgur eocensis*. See also Harris (1899) 65. *pl. 8, f. 18;* as *Triton* (*Ranularia*) *eocensis*.

congeneric with that of Aldrich, has considered *Pseudoperissolax* a subjective synonym of *Perissolax*.

An examination of the figures of "*Perissolax*" *eocensis* shows that the aperture possesses an outer lip which is strongly denticulate internally, that there are folds on the columella, and that the aperture is so constricted at the base that the anterior canal is sharply delimited. None of these characters are to be observed in *Pseudoperissolax blakei*.

The type of *Perissolax trivolva* has been refigured by Whitfield.* It is an internal cast, and the presence or absence of a denticulate outer lip or of columellar folds is not apparent. If the other specimen figured by Whitfield is conspecific, Gabb's species possesses a moderately well developed axial sculpturing. The spire is also much lower than has been observed in *Pseudoperissolax*.

The nucleus of *P. blakei* is rather large, elevated, of at least 5 smooth, shouldered, convex whorls. It is here figured: PLATE 19, FIGURE 9 (Hypotype 15840; loc. 7200, Tejon formation; length 10.0 mm., diameter 6.6 mm.).

Pseudoperissolax blakei (Conrad) praeblakei NEW SUBSPECIES

PLATE 19, FIGURES 14, 22

Perissolax blakei Gabb (1864) 92 (in part). *pl. 21, f. 110.* Not *P. blakei* Conrad.†
Perissolax blakei (Conrad); Dickerson (1916) 433, 451 (between Domengine and Cantua creeks).
Pseudoperissolax blakei (Conrad) n. subsp. Clark (1921) 159 ("Meganos" north of Coalinga).
Pseudoperissolax blakei (Conrad) n. var. ? Clark (1926) 116 (Coalinga).
Pseudoperissolax blakei (Conrad); Clark in M. A. Hanna (1927) 260 (Coalinga).
Pseudoperissolax blakei (Conrad) (subsp. ?) Stewart (1927) 429. *pl. 28, f. 1* (partial synonymy).
Pseudoperissolax blakei (Conrad) var. Merriam & Turner (1937) 94, 96, 100 (Lillis Ranch).

Holotype 15799; loc. 1817; length (incomplete) 23.6 mm., diameter 24.2 mm.
Paratype 15800; loc. 1817; length (incomplete) 24.6 mm., diameter 14.5 mm.

The older Eocene species which have been referred to *Pseudoperissolax blakei* (Conrad) differ from the typical (Tejon) form in having a flatter shoulder on the whorl, which does not extend as high on the preceding whorl, giving the appearance of a higher spire. The anterior angulation is generally more strongly developed and is almost equal to the posterior in strength, so that the area between the angulations is more nearly parallel to the axis of the shell.

The development of the sloping shoulder and the reduction in strength of the anterior angulation appears to be a progressive character which can be traced from the Martinez species *P. tricarinata*

* Whitfield (1892) *pl. 21, f. 1.*
† Conrad (1858) 322. *pl. 2, f. 13;* as *Busycon ? blakei.*

(Weaver*), in which the shoulder is almost at right angles to the axis of the shell, and there are 2 angulations of equal strength, with a third (weaker) anterior carina. This third carina is often slightly developed on the specimens from the Capay stage, but is indicated on the Tejon specimens only by a stronger spiral thread.

Suborder TAENIOGLOSSA

Family CYMATIIDAE

Genus CYMATIUM (Bolten) Roeding 1798

GENOTYPE (by subsequent designation, Dall 1904): *Cymatium femorale* (Linnaeus) = *Murex femorale* Linnaeus. Recent, West Indies (*fide* Woodring).

Subgenus LAMPUSIA Schumacher 1817

TYPE SPECIES (by subsequent designation, Herrmannsen, 1847): *Tritonium pileare* (Linnaeus) = *Murex pileare* Linnaeus. Recent, Mediterranean Sea and other localities (*fide* Woodring).

Cymatium (Lampusia) NEW SPECIES

PLATE 19, FIGURE 8

? *Nyctilocthes ? californicus* Gabb n. var. Clark (1926) 116 (Coalinga).

Figured specimen 15802; loc. 672; length (incomplete) 16.8 mm., diameter (incomplete) 9.6 mm.

A fragmentary shell from loc. 672, lacking the nucleus and most of the body-whorl, represents a species of *Lampusia* which is also represented by poorly preserved material from the Llajas formation (U. C. loc. 7003) and the La Jolla formation (U. C. loc. 5062). On the two spire-whorls preserved there are 5 rows of rounded nodes arranged along 5 primary spirals, one above the other, with 3 to 5 microscopic secondary riblets in the interspaces. The portion of the body-whorl present shows 8 rows of nodes with approximately 7 secondary riblets. Strong varices extend from the base of the whorl to the suture. The anterior canal appears to have been of moderate length and projecting dorsally.

Family TRITONIDAE?

Genus CUMIA Bivona 1838

GENOTYPE (*fide* Cossmann): *Cumia decussata* Bivona = *Triton reticulatus* Blainville. Recent, Mediterranean Sea and Galapagos Islands (*fide* Reeve). (Tryon, Conch. Icon., doubts the Galapagos Islands reference.)

* Weaver (1905) 121. *pl. 13, f. 9;* as *Perissolar "tricarnatus."*

Cumia harrisi (Dickerson)

PLATE 19, FIGURE 16

Metula harrisi Dickerson (1916) 426, 427, 433 (loc. 672 in error), 450, 494, *pl. 42, f. 1* (not 7), (described, loc. 1817).—Clark (1921) 159 ("Meganos" north of Coalinga).—Woodring (1928) 285, 286 (not *Metula, sensu stricto*). Not *Metula harrisi* Olsson (1922) 288. *pl. 10, f. 10* (renamed *Metula olssoni* Woodring (1928) 287).
Metula "harrissi" Dickerson; Clark (1926) 116 (Coalinga).

Topotype 15899; loc. 1817; length (incomplete) 12.4 mm., diameter 5.8 mm.

Clark's record of *Metula "harrissi"* from the Domengine formation is apparently based upon Dickerson's erroneous listing of this species from loc. 672. There appears to be no material justifying its consideration as a Domengine species.

Family BURSIDAE

Genus RANELLA Lamarck 1816

GENOTYPE (by subsequent designation, Children 1823): *Ranella gigantea* Lamarck. Recent, Mediterranean Sea.

Ranella domenginica NEW SPECIES

PLATE 19, FIGURES 6, 20

Syntype 15803; loc. 672; length (incomplete) 40.0 mm., diameter 23.0 mm.
Syntype 15804; loc. 672; length (incomplete) 27.9 mm., diameter (incomplete) 18.8 mm.

DESCRIPTION.—Shell moderately large, thin, of 6 or 7 post-nuclear whorls; spire-whorls angulate medianly, sculptured with axial and spiral ribbing, and with numerous irregularly-spaced varices extending continuously across the whorl; axial sculpture consisting of 10 to 12 swollen ribs which are most strongly developed on the upper portion of the whorl and at the angulation, where they tend to form prominent subspinose nodes; spiral sculpture consisting of primary, secondary, and tertiary threads, the angulation marked by a strong primary with 2 primaries anterior, the lowest obscured by the appressed, irregular suture; a prominent secondary rib between the primaries separated from the primary above and below by 2 tertiary riblets; 4 primary spirals posterior to the angulation with a secondary inter-rib between each pair and separated from them by a single microscopic tertiary riblet; body-whorl similarly sculptured, but the whorl tending to be biangulate, a second angulation appearing at the line of the second primary spiral anterior to the median angulation of the spire; axial ribbing less prominently developed on the shoulder of the whorl and obsolete anterior to the line of nodes on the posterior angulation.

The apertural features are not well preserved on the type specimens. Supplementary material from loc. 7003, Llajas formation, Simi Valley,

enables the following description to be given; Aperture lunar: outer lip thickened, reflected, denticulate, and grooved posteriorly for the anal siphon; columella callused, bearing 3 prominent folds anteriorly; anterior canal short, narrow, very slightly recurved.

COMPARISON.—*R. domenginica* differs from *R. washingtoniana* Weaver* in possessing a less recurved anterior canal, a more strongly denticulate inner lip in which the denticles are not arranged in pairs, and a well-developed posterior notch for the anal siphon; the axial scuplturing is more strongly developed posterior to the angulation of the spire-whorl, and less strongly developed anteriorly; between each pair of the primary spirals anterior to the angulation on *R. washingtoniana* are 3 secondaries separated each from each by one or two tertiaries, while posteriorly there may be as many as 3 tertiary riblets alternating with single stronger spirals; the growth-lines are more strongly developed and give a beaded effect to the spiral ribbing. *R. cowlitzensis* Weaver† has a more sharply recurved anterior canal, a larger number of columellar folds, and a less prominently developed posterior notch; while there are 2 rows of broadly rounded nodes on the spire and 3 on the body-whorl.

Genus RANELLINA Conrad 1865

GENOTYPE (by monotypy): *Ranella maclurii* Conrad. Eocene, Claiborne, Alabama.

Ranellina pilsbryi Stewart

PLATE 19, FIGURES 10, 17

Fusus californicus (Conrad); Gabb (1864) 85, 86. *pl. 28, f. 205, a* (Tejon). Not *Clavatula ? californica* Conrad (1855) 11.
Nyctilochus hornii (Gabb); Dickerson (1916) 433, 451. *pl. 42, f. 3* (loc. 672). Not *Tritonium hornii* Gabb (1864) 94. *pl. 28, f. 208* (Tejon).
Clavilithes californicus (Conrad); Anderson & Hanna (1925) 63. *pl. 13, f. 1, 2* (Tejon).
Ranellina pilsbryi Stewart (1927) 384, 385. *pl. 30, f. 8, 9* (described, Tejon).

Hypotype 15805; loc. 672; length 23.8 mm., diameter 12.0 mm.
Hypotype 15806; loc. 672; length 12.8 mm., diameter 6.5 mm.

The Domengine specimens appear to have a proportionally lower spire than do the Tejon forms, and the outer lip tends to be denticulate internally, the denticles occurring at a point opposite the varices.

Dickerson's figure‡ of "*Nyctilochus hornii*" is natural size, not "× 2" as indicated.

* Weaver (1912) 41. *pl. 2, f. 14.*
† Weaver (1912) 41. *pl, 2, f, 15; pl, 3, f. 26, 27.*
‡ Dickerson (1916) *pl. 42, f. 3.*

Family CASSIDIDAE

Genus GALEODEA Link 1807

GENOTYPE (by monotypy): *Buccinum echinophorum* Linnaeus. Recent, Mediterranean Sea.

The genus *Galeodea* appears to be one of the most significant "index" fossils in the Eocene deposits of California. Three distinct species occur in the collections from the Coalinga area. No two of the species occur together and each appears to be characteristic of the zone in which it is found. The following stratigraphic relationship is to be noted:

Domengine formation.......... *G. tuberculiformis* Hanna.
Arroyo Hondo fmtn. (up. zone)... *G. susanae* Schenck.
Arroyo Hondo fmtn. (l. zone). ... *G. sutterensis* Dickerson.

In the Tejon and Cowlitz formations *G. trituberculata* (Weaver) occurs, while in the Meganos formation are *G. sutterensis meganosensis* n. subsp. (page 151) and an undescribed species which is characterized by possessing a very long canal, 3 strongly noded carinae with 12 nodes on the shoulder row, and a very high spire which the nearly flat shoulder of the preceding whorl contacts but slightly above the central carina.

Galeodea tuberculiformis Hanna

PLATE 19, FIGURES 19, 21, 23, 24, 25, 26, 27

Morio (*Sconsia*) *tuberculatus* Gabb (1864) 104. *pl. 19. f. 57* (described, Domengine fmtn., Martinez).—Gabb (1869) 223 (Griswold's).—Turner & Stanton (1894) 95 (New Idria).—Stanton (1896) 1027 (New Idria).—Turner in Anderson (1908) 10 (New Idria).
Morio tuberculatus Gabb; Anderson (1905) 166 (north of Los Gatos Creek).
Galeodea tuberculata (Gabb); Dickerson (1916) 433. *pl. 42, f. 2* (between Domengine and Cantua creeks). Not *Cassidaria tuberculata* Risso (1826) 186 (= *Galeodea*).
Galeodea tuberculiformis Hanna (1924) 167 (new name for *Morio* (*Sconsia*) *tuberculatus* Gabb). —Anderson & Hanna (1925) 110 (not at Tejon).—Schenck (1926) 83. *pl. 14, f. 12-16* (redescribed).—Stewart (1927) 380. *pl. 28, f. 11* (lectotype and synonymy).
Galeodea tuberculiformis (Hanna) = *G. tuberculata* Gabb; Clark (1926) 115 (Coalinga).

Hypotype 15807; loc. 672; length (incomplete) 32.0 mm., maximum diameter 23.9 mm.
Hypotype 15808; loc. 672; length (incomplete) 18.5 mm., maximum diameter 17.9 mm.
Hypotype 11783; loc. 672; length (incomplete) 20.2 mm., maximum diameter 14.5 mm.
Hypotype 15809; loc. 672; length (incomplete) 16.9 mm., maximum diameter (incomplete) 12.8 mm.
Hypotype 15810; loc. 672; length (incomplete) 14.5 mm., maximum diameter 11.3 mm.
Hypotype 15811; loc. 672; length (incomplete) 9.8 mm., maximum diameter 7.7 mm.

In all the specimens examined the rostrum of the anterior canal is broken, so that in all cases the length must be considered to be essentially incomplete. If Wrigley's conclusions that all the Eocene forms possessed a rostrum similar to that which he figures for *Galeodea*

enodis (Deshayes)* are to be accepted, the length of all specimens, complete, would be several millimeters longer.

This species may be distinguished from all other West Coast species of *Galeodea* in the possession of a well-developed series of denticles on the outer lip, which is reflected and thickened. Varices on the earlier whorls of the shell are almost universally present, and were observed on all the specimens examined, although Schenck† notes that they may be absent.

The protoconch is naticoid, consisting of 4 smooth whorls, slightly tabulate at the impressed suture. The first succeeding whorl is characterized by 3 well-developed spiral riblets, the sutural riblet being smooth, the anterior two nodose. Approximately one third of the circumference from the end of the protoconch longitudinal ribs appear in the interspaces. On the succeeding whorls fine intercalated spiral threads appear, the nodose character of the most anterior thread becomes accentuated while the middle thread tends to appear beaded, loses its primary distinctness, and is not separable from the other threads on the shoulder of the body-whorl.

The number of nodose carinae on the body-whorl varies. On the smallest specimen examined the shoulder of the whorl alone is carinated. This is the anterior riblet of the post-nuclear whorl. The other specimens show 2 or 3 carinae. When the anterior carina is not noded its position is marked by a spiral thread, which is slightly stronger in its development than the normal threads on that portion of the whorl.

Galeodea susanae Schenck

Galeodea susanae Schenck (1926) 85. *pl. 15, f. 3–7* (described, Simi Valley).

Galeodea sutterensis Dickerson

Plate 19, figure 15

Morio tuberculatus "Gabb"; Dickerson (1913) 264 (Marysville Buttes).
Galeodea sutterensis Dickerson (1916) 492. *pl. 40, f. 1 a, b* (described, Marsyville Buttes).—Merriam & Turner (1937) 94, 100 (Lillis Ranch). Not *Galeodea sutterensis* Dickerson; Clark & Woodford (1927) 113. *pl. 19, f. 21* (Meganos formation).
Cassidaria "sufferensis" Cossmann (1916) 110.

Hypotype 15812; loc. 1817; length (incomplete) 27.5 mm., maximum diameter 21.4 mm.

A re-examination of the holotype of this species indicates that the shoulder of the body-whorl is marked by 8 or 9 spinose nodes (rather than 14). The statement of Clark & Woodford‡ that the type has

* Wrigley (1934) 123. *pl. 17, f. 33, 34.*
† Schenck (1926) 83.
‡ Clark & Woodford (1927) 113.

3 well-developed nodes on the body-whorl should be corrected to read "rows of nodes." The protoconch is similar to that of *G. tuberculiformis*. The first post-nuclear whorl is marked by 9 rounded spiral threads, separated by interspaces of slightly less than equal width. On the second post-nuclear whorl the number of threads has increased by intercalation to 14, and 2 have become more strongly developed and nodose. On the third whorl the anterior thread forms the noded carina at the shoulder, the other has not been strengthened, and a third thread of equal strength has developed between the two. (This is the condition noted on the body-whorl of *G. sutterensis meganosensis* n. subsp., below.) On the body-whorl only the anterior thread is present as the shoulder-carina, and 2 additional noded carinae are present on the middle portion of the whorl. The other threads have lost their identity and are not separable from the other threads on the whorl.

The aperture is not denticulate, although a swelling near the posterior canal may be considered as representing the posterior denticle which is the most strongly developed on *G. tuberculiformis*.

The form figured by Clark & Woodford (*op. cit.*) as this species is distinct, and is here described.

Galeodea sutterensis Dickerson meganosensis NEW SUBSPECIES

PLATE 19, FIGURE 18

Galeodea sutterensis "Dickerson"; Clark & Woodford (1927) 113. *pl. 19, f. 21* (Meganos formation).

Holotype 31244; loc. 3152; length (incomplete) 33.0 mm., maximum diameter 28.0 mm.

DESCRIPTION.—Shell large, heavy, with 2 rows of spinose tubercles on the body-whorl, the carina on the shoulder marked by 11 or 12 nodes, those of the second carina being offset in relation to those of the shoulder carina; below each carina are 2 strong spiral threads, the anterior being best developed; body-whorl distinctly angulate at the anterior carina; shoulder of the whorl flattened, curving up sharply to the appressed suture; spire high, the shoulder-carina being well above the suture. Nuclear and early post-nuclear whorls not seen; canal similar to *G. sutterensis*.

COMPARISON.—This subspecies differs from *G. sutterensis* in possessing but 2 nodose carinae, which have a greater number of nodes. (The body-whorl is more angulate at the second carina). Below the nodes are well-developed spiral threads; these are absent on the body-whorl of *G. sutterensis* but seem to have been present on the penulti-

mate whorl, which appears to agree with the geologic occurrence of these forms in that the subspecies *meganosensis* is ancestral to *G. sutterensis*. The shoulder of the new form is relatively flatter, and the spire higher.

Family FICIDAE

Genus FICOPSIS Conrad 1866

GENOTYPE (by subsequent designation, Stewart 1927): *Hemifusus remondii* (Gabb). Eocene, California.

In his study of the English Eocene *Ficidae*, Wrigley* refers the forms similar to those here considered to represent the genus *Ficopsis*, together with "*Pyrula*" *intermedia* Melleville, the type of *Priscoficus* Conrad (by subsequent designation, Stewart 1927), to the genus *Ficus* Bolten (type, by tautonomy, *Bulla ficus* Linnaeus), preferring to consider them as "groups" of that genus. The geologic range of these "groups" seems to be significant. *Priscoficus* is a Paleocene form, which may be represented in the higher Eocene horizons by *Ficopsis meganosensis* and its subspecies *packardi*, and certain other nodosely carinated species. These all have a higher spire than is typical of *Priscoficus*, and are here referred to *Ficopsis*. *Ficopsis* (*sensu stricto*) first appears on the West Coast and in Europe in the Eocene, and, according to Wrigley, appears finally to have disappeared with the Miocene *F. burdigalensis*, the type of *Fulguroficus* Sacco, while *Ficus* (*sensu stricto*), which first appeared in the Middle Eocene, has persisted to the Recent. It is the opinion of the writer that forms as distinct at the time of first appearance as *Ficus* and *Ficopsis* should be considered to represent separate generic lines of development.

Ficopsis remondii (Gabb) crescentensis Weaver & Palmer

Fusus (*Hemifusus*) *remondii* Gabb (1864) 87 (in part). *pl. 18, f. 36*.

Fusus remondii Gabb; Arnold (1909) 13. (south of Los Gatos Creek).—Arnold & Anderson (1910) 71 (south of Los Gatos Creek).

Ficopsis remondii (Gabb); Conrad (1866) 15, 36 (new genus).—Gabb (1869) 158, 221 (Griswold's).—Stanton (1896) 1027 (New Idria).—Dickerson (1916) 427, 433, 449 (between Domengine and Cantua creeks).—Clark in M. A. Hanna (1927) 260 (Coalinga); Stewart (1927) 376 (synonymy).

Ficopsis angulatus Weaver (1905) 119. *pl. 13, f. 5* (described, south of Martinez). Not *Pyrula angulata* Edwards (1866) *pl. 4* (= *Ficopsis*).

Ficopsis remondii Gabb n. var. Clark (1921) 159 ("Meganos" north of Coalinga).

Ficopsis remondii angulata (Weaver); Clark (1926) 115 (Coalinga).—Stewart (1927) 377.

Ficopsis remondii (Gabb) var. *crescentensis* Weaver & Palmer (1922) 39. *pl. 11, f. 14* (described, Port Crescent, Washington).—Stewart (1930) 41.—Merriam & Turner (1937) 100 (loc. 1817).

* Wrigley (1929) 235–251.

The tricarination of the body-whorl, which is characteristic of the subspecies *crescentensis*, is observable to a slight extent on some of the species from the Tejon, but is never as strongly developed as it is on the specimens from the Middle Eocene horizons.

There is a marked resemblance between this subspecies and *Ficopsis penitus* (Conrad) from the Claiborne formation, which appears to have an ancestor in the Wilcox formation. The *Ficopsis remondii* line first appears in the Capay stage and it is suggested that the Wilcox form may have been ancestral to the West Coast species as well as the Claiborne type.

Ficopsis meganosensis Clark & Woodford packardi Merriam & Turner

PLATE 19, FIGURES 11, 13

Ficopsis cf. *hornii* Gabb; Dickerson (1916) 426 (loc. 1817).
Ficopsis cf. *cowlitzensis* Weaver; Dickerson (1916) 433 (loc. 1817).
Ficopsis meganosensis var. *packardi* Merriam & Turner (1937) 102. *pl. 6, f. 7* (described, Oregon).

Hypotype 15813; loc. 1817; length (incomplete) 17.6 mm., diameter 10.0 mm.
Hypotype 15814; loc. 1817; length (incomplete) 14.6 mm., diameter 10.5 mm.

Family **CYPRAEIDAE**

Genus **EOCYPRAEA** Cossmann 1903

GENOTYPE (by original designation): *Cypraea inflata* Lamarck. Lutetien-Bartonian, Paris Basin, France.

The family *Cypraeidae* has been the subject of extensive monographs by Jousseaume,* Cossmann,† Vredenburg,‡ and Schilder.§ All have neglected, in general, the fossil West American species, which have suffered from a similar lack of attention from western students. Of the above monographs, that of Vredenburg with additions and corrections by Schilder seems to be the most satisfactory at the present time and is followed here.

The name *Eocypraea* was proposed by Cossmann as a section of *Cypraea* (*sensu stricto*)¶. Vredenburg, on the basis of morphological characters as well as geologic range, has made *Eocypraea* a distinct

* Jousseaume (1884) 81–100.
† Cossman (1903) 143–185.
‡ Vredenburg (1920) 65–152.
§ Schilder (1926a) 375.
¶ All the above authors have considered *C. mappa* Linnaeus as the genotype species. Jousseaume and Cossmann date the designation from Lamarck's "Prodrome," 1799. By an opinion of the Committee on Nomenclature, no. 79, Lamarck's examples are not considered valid type designations. The first valid designation appears to be that of Montfort 1810, who accepted *C. tigris* Linnaeus as the type species. This reduces to synonymy *Mauritia*, and *Tigris* Troschel, 1863.

The typical variety, as indicated by the topotype material from near New Idria, is of small size, the specimen figured being the largest in the collections. It is ornamented with 11 to 16 longitudinal ribs which, in the majority of specimens, extend completely across the body-whorl, and are adjacent on the whorls, giving the appearance of extending continuously up the spire. On a few of the topotypes the ribs are obsolete on the base of the body-whorl. The spiral ribbing tends to be uniformly well developed.

The specimens from the Reef Ridge section attain a much greater size, and show a great amount of variation in the nature of the longitudinal ribbing. On the majority of individuals the ribs do not extend onto the base of the body-whorl, and in many instances (PLATE 20, FIGURE 4) they are elevated with a tendency to shorten into nodes. This condition is marked on the last 2 or 3 ribs on the body-whorl of the larger specimens. On these, also, the spiral ribbing tends to be obsolete on the body-whorl.

Rimella (Macilentos) macilenta White oregonensis Hendon

PLATE 20, FIGURES 6, 10

Rimella canalifera "Gabb"; Anderson in Dumble (1912) 32 (Salt Creek).—Dickerson (1916) 433 (in part) (loc. 1817).
Rimella simplex Gabb; Dickerson (1916) 427, 452 (loc. 1817).
Rimella (*Macilentos*) *macilenta oregonensis* Hendon in Turner (1938) 94. *pl. 18, f. 1–4.*

Holotype 33633; loc. U. O. 142; length 15.5 mm., diameter 6.6 mm.
Paratype 33187; loc. 3608; length 21.7 mm., diameter 8.0 mm.

The subspecies *oregonensis* may be distinguished from typical *R. macilenta* by the smaller number of axial ribs and more slender outline. The subspecies generally has 9 to 11 axials while the typical form may have from 12 to 16. In *oregonensis* these ribs are sharper and more elevated, with a tendency to shorten into nodes on the adult whorls.

Abundant but poorly preserved specimens in the collections from locality 1817 appear to be referable to this subspecies.

Genus TEREBELLUM (Bolten) Roeding 1798

GENOTYPE (by tautonomy): *Bulla terebellum* Linnaeus (renamed *Terebellum subulatum* Lamarck 1801). Recent: China Sea, Indian and Philippine Archipelagos. (Reeve.)

The West Coast species of this genus have been referred to *Seraphs* Montfort 1810 (type, *Terebellum convolutum* Lamarck). In this group the spire is completely covered by the later whorls and the aperture extends the full length of the shell. In *Terebellum* the spire is not covered by the later whorls.

Terebellum californicum NEW SPECIES

PLATE 20, FIGURES 7, 8, 11

Seraphs erratica "(Cooper)"; Clark (1926) 116 (Coalinga).—Clark in M. A. Hanna (1927) 260 (Coalinga).

Holotype 15820; loc. A-976; length (incomplete) 26.8 mm., diameter 7.9 mm.
Paratype 15821; loc. A-1164; length 20.6 mm., diameter 5.8 mm.
Hypotype 15822; loc. 3296 (east of Simi Valley); length (incomplete) 31.4 mm., diameter 9.0 mm.

DESCRIPTION.—Form cylindric; spire immersed, only the last four whorls visible; suture linear, indistinct; outline of shell slightly convex toward the base, this tending to be twisted dorsally; aperture long and narrow, closely appressed to the spire posteriorly and broad at the base; surface smooth.

COMPARISON.—This species has been referred to "*Tornatina*" *erratica* Cooper,* which is described as being "deeply channeled at the sutures." The sutures in *T. californicum* are linear and so indistinct as to be visible with difficulty. *Seraphs andersoni* Dickerson,† from the Oligocene of Washington, is more inflated than the Eocene species. *Seraphs (?) thompsoni* Dickerson,‡ from the Martinez horizon, probably does not belong in the *Strombidae*, and is certainly neither a *Seraphs* nor a *Terebellum*.

Family CLAVIDAE (CERITHIIDAE)

Genus POTAMIDES Brongniart 1810

GENOTYPE (by monotypy): *Potamides lamarcki* Brongniart. Oligocene, Ormoy.

Potamides carbonicola Cooper

PLATE 20, FIGURES 23, 24, 25, 26, 27

Potamides carbonicola Cooper (1894) 44. *pl. 1, f. 14–19.* (Described as *Cerithidea carbonicola* Cooper on plate legend.)—Stanton (1896) 1027 (New Idria).—Arnold (1909) 14. *pl. 4, f. 2, 3* (San Joaquin Coal Mine).—Arnold & Anderson (1910) 71. *pl. 26, f. 2, 3* (San Joaquin Coal Mine).—Dickerson (1916) 451 (Coalinga District).

Topotype 15823; loc. 7155; length (incomplete) 23.9 mm., diameter 9.8 mm.
Hypotype 15824; loc. A-1020; length (incomplete) 23.0 mm., diameter 10,7 mm.
Hypotype 15825; loc. A-1020; length (incomplete) 25.0 mm., diameter 10.5 mm.
Hypotype 15826; loc. A-1020; length (incomplete) 25.2 mm., diameter 13.0 mm.
Topotype 15827; loc. A-1223; length (incomplete) 21.9 mm., diameter 14.7 mm.

The great range of variation within this brackish-water species is shown in the specimens figured. The noded form (topotype 15823)

* Cooper (1894) 47. *pl. 2, f. 35.*
† Dickerson (1917) 180. *pl. 31, f. 9 a, b.*
‡ Dickerson (1914a) 144. *pl. 14, f. 6 a, b.*

greatly resembles *P. tristriatus* (Lamarck) of the Paris Basin Lutetian. The range of variation in that species is not known.

Genus BITTIUM Leach; Gray (October) 1847

GENOTYPE (by subsequent designation, Gray, November 1847): *Murex reticulatus* Montagu = *Strombiformis reticulatus* Da Costa. Recent, Mediterranean Sea.

Bittium (?) dumblei (Dickerson)

PLATE 20, FIGURE 3

Cerithiopsis alternata Gabb (1864) 116. *pl. 21, f. 114, a* (described, Martinez).—Dickerson (1916) 432, 448 (between Domengine and Cantua creeks).—Clark (1926) 115 (Coalinga). Not *Bittium alternatum* (Say).*

Cerithiopsis dumblei Dickerson (1916) 432, 489. *pl. 38, f. 12* (described, loc. 672).—Cossmann (1916) 110 (said to resemble *Bittium*).—Clark (1926) 115 (Coalinga).

Cerithium dumblei (Dickerson); Stewart (1927) 354. *pl. 26, f. 15* (lectotype of *Cerithiopsis alternata*, and synonymy).

Topotype 15828; loc. 672; length (incomplete) 11.3 mm., diameter 4.6 mm.

The holotype of *Cerithiopsis dumblei* Dickerson, though immature, does show faint secondary spirals on the body-whorl. The specimen figured, a topotype of Dickerson's species, shows the secondary spirals strongly developed, as well as the numerous varices which appear to be characteristically developed in *Bittium reticulatum* (Da Costa), the type of the genus.

Dickerson's statement concerning the nuclear whorls is not relevant as they are so décolleté that it is not beyond possibility that the whorls in question are post-nuclear and that the nucleus is entirely broken. If they are to be considered nuclear whorls, they are much larger than is characteristic of *Bittium*, and the species might be referable to *Newtoniella* Cossmann 1893 (type, *Cerithium clavus* Lamarck) from the Paris Basin Eocene. The anterior canal of *B.* (?) *dumblei* appears to be shorter than is characteristic of that genus. The aperture of the holotype of *C. dumblei* is broken anteriorly, giving the figures the appearance of a longer canal than is actually the case, although a definite canal is present.

Stewart referred this species to *Cerithium* Bruguière 1789, without stating any definite reasons for so doing. The type of *Cerithium* (by subsequent designation, Montfort 1810), *Cerithium virgatum* Montfort (= *Murex vertagus* Linnaeus), makes *Cerithium* a synonym of *Clava* Martyn 1784, type (by subsequent designation, Pilsbry 1901) *Clava rugata* Martyn. Stewart (1927: 355) discusses the question, and concludes that by a rather strained interpretation of tautonomy *Cerithium adansonii* Bruguière ("*Le Cerite*" of Adanson) could be considered

* Say (1822) 243; as *Turritella alternata*.

the type. It is not likely that such an interpretation can stand against a valid subsequent designation. Cossmann* has reproduced Adanson's figures, and states that he considers that the form figured belongs to the brackish-water genus *Pyrazus* Montfort.†

Family MELANIIDAE

Genus LOXOTREMA Gabb 1868

GENOTYPE (by monotypy): *Loxotrema turrita* Gabb. Eocene, Domengine formation, California.

Loxotrema turrita Gabb

PLATE 20, FIGURES 15, 16, 17, 18, 19

Loxotrema turrita Gabb (1868) 147. *pl. 14, f. 21* (type of *Loxotrema* Gabb).—Gabb (1869) 168, 227. *pl. 28, f. 49* (described, "ten miles west of Griswold's").—Arnold (1909) 14. *pl. 4, f. 17* (San Joaquin and California Coal Mines).—Arnold & Anderson (1910) 71. *pl. 26, f. 17* (San Joaquin and California Coal Mines).—Dickerson (1916) 450 (Coalinga and 10 miles W. of Griswold's).—Clark (1926) 115 (Coalinga).—Stewart (1927) 347. *pl. 26, f. 3, 4* (lectotype and synonymy).

Topotype 15829; loc. A-1154; length (incomplete) 30.0 mm., diameter 14.4 mm.
Topotype 15830; loc. A-1154; length (incomplete) 24.9 mm., diameter 11.8 mm.
Topotype 15831; loc. A-1154; length (incomplete) 7.6 mm., diameter 5.0 mm.
Hypotype 15832; loc. A-1020; length (incomplete) 34.0 mm., diameter 17.6 mm.

The nature of the nuclear whorls is not known in this species. On what is apparently the first post-nuclear whorl the shell is marked by 3 spiral ribs, the anterior pair being the stronger, and by several longitudinal ribs which are strongly nodose at the junction with the spiral ribbing; on the third whorl the posterior spiral rib becomes as strong as the others and the longitudinal ribbing disappears, but the spiral ribs continue to be nodose; on the fourth whorl the median spiral rib disappears, the whorl becoming flat-sided, the anterior and posterior ribs of equal strength and tending to lose their nodose character. The posterior rib forms the tabulate shoulder of the whorl, the anterior rib tends to be lost on the later whorls, and is visible only as a slight rounding of the whorl toward the suture. On some specimens (hypotype 15832), the nodose character of the posterior spiral rib persists throughout the development of the individual.

This is a brackish-water species, and in all its occurrences is associated with *Ostrea idriaensis* Gabb and *Potamides carbonicola* (Cooper).

Family "RISSOINIDAE"

Genus KEILOSTOMA Deshayes 1848

GENOTYPE (by monotypy ?): *Melania marginella* Lamarck = *Bulimus turricula* Bruguière. Eocene, Paris Basin, France.

* Cossmann (1906) 66. *pl. 1, f. 3, 4*.
† For a more complete discussion see: Cox (1927) 84, 85.—Woodring (1928) 333.

Cossmann* and others have used *Paryphostoma* Bayan 1873, for this genus in the belief that *Keilostoma* Deshayes was a homonym of *Chilostoma* Fitz 1833. Under Article 36, Recommendations, of the International Rules of Zoological Nomenclature, Deshayes' name is not invalidated by that of Fitz (see also Opinion 25).

Keilostoma californicum NEW SPECIES

PLATE 20, FIGURES 12, 13

Holotype 15833; loc. A-819; length (incomplete) 11.0 mm., diameter 4.0 mm.
Paratype 15834; loc. A-976; length (incomplete) 12.1 mm., diameter 4.0 mm.

DESCRIPTION.—Shell small, turrited, heavy, the number of whorls not known (9+); whorls but slightly convex with an inconspicuous collar-like concavity below the sutural band, ornamented by deeply incised lines separated by interspaces of regular width (8 lines on the penultimate whorl and 20 on the body-whorl of the holotype); whorls appressed; sutures linear, slightly tabulate; aperture rounded, entire, with a small posterior canal; outer lip thickened; inner lip heavily callused.

COMPARISON.—This is the first species of this genus to be described from the American Pacific Tertiary deposits. It resembles *Keilostoma minor* Deshayes† from the Lutetian of the Paris Basin, but differs from that species in possessing a greater number of incised lines on the whorls, and in having a thinner callus-thickening on the outer lip. *Keilostoma mediavia* Harris,‡ from the Midway horizon of the Gulf Coast, is not striated.

No figures of *Keilostoma subturricula* Cox§ from the Laki formation of India were available to the writer so that adequate comparison is impossible, but as described it appears to be a closely related species, differing only in possessing 22 lines on the body-whorl and 8 on the spire-whorls, separated by subequal interspaces.

Family TURRITELLIDAE

Genus TURRITELLA Lamarck 1799

GENOTYPE (by monotypy): *Turbo terebra* Linnaeus. Recent.

Turritella andersoni Dickerson

Turritella pachecoensis "Stanton"; Anderson (1908) 13 (Salt Creek).—Anderson in Dumble (1912) 32 (Salt Creek).

* Cossmann (1921) 70.
† Deshayes (1861) 425.
‡ Harris (1896) 230. *pl. 12, f. 8, 9, a.*
§ Cox (1931) 47.

Turritella andersoni Dickerson (1916) 427, 434, 453, 501. *pl. 42, f. 9 a, b* (described, loc. 1817). —Clark (1921) 159, 161 ("Meganos," north of Coalinga).—Clark in M. A. Hanna (1927) 260 (Coalinga).—Merriam & Turner (1937) 94, 100 (loc. 1817).

This species is not known with certainty from the Domengine formation in the Coalinga district, although some forms, here referred to the subspecies *lawsoni*, are intermediate between the typical form and that subspecies.

It is exceedingly abundant at the type locality (loc. 1817), in the lower portion of the Arroyo Hondo formation, and also occurs in the Capay Valley, and in the same horizon in the Oregon Eocene.

Turritella andersoni Dickerson lawsoni Dickerson

? *Turritella saffordi* Gabb; Cooper in Watts (1894) 62 (north of Los Gatos Creek).—Watts in Anderson (1908) 15 (north of Los Gatos Creek).

? *Turritella pachecoensis* Stanton; Anderson (1905) 164, 166 (Avenal sandstones and north of Los Gatos Creek).

Turritella pachecoensis Stanton; Arnold (1909) 14. *pl. 4, f. 14* (north of McLure Valley).—Arnold & Anderson (1910) 71. *pl. 26, f. 14* (north of McLure Valley).

Turritella lawsoni Dickerson (1916) 434, 502. *pl. 42, f. 10 a, b* (described, Domengine Ranch). —Clark in M. A. Hanna (1927) 260 (Coalinga).

This subspecies was described from material labeled as derived from a float boulder in Domengine Creek, Sec. 24, T. 18 S., R. 15 E. The matrix most closely resembles that of the upper zone of the Ragged Valley shale member, but it has not been found in place. It has been found in the Domengine near the southern limits of the Reef Ridge exposure and was figured by Arnold as *Turritella pachecoensis* from this area.

Turritella buwaldana Dickerson

Turritella uvasana Conrad; Gabb (1869) 228 (in part), (Griswold's).—Stanton (1896) 1027 (New Idria).—Dickerson (1915) *pl. 5, f. 1 a* (loc. 672).—Dickerson (1916) 434 (in part). *pl. 42, f. 6* (between Domengine and Cantua creeks).

Turritella buwaldana Dickerson (1916) 434, 453, 500. *pl. 42, f. 7 a, b* (described, loc. 672).—Clark in M. A. Hanna (1927) 260 (Coalinga).—Merriam MS. (discussion).

Turritella uvasana buwaldana Dickerson; Clark (1926) 116 (Coalinga).

Turritella kewi Dickerson (1916) 434, 453, 501. *pl. 42, f. 8* (described, loc. 672).

This is the most abundantly represented *Turritella* in the Domengine collections. A specimen in Gabb's material from "10 miles W. of Griswold's" is of this species. With the exception of one or two specimens of *T. andersoni lawsoni*, this is the only species of *Turritella* in the Vallecitos collections.

Turritella buwaldana Dickerson crooki Merriam & Turner

Turritella buwaldana crooki Merriam & Turner (1937) 105. *pl. 5, f. 6* (described, Capay Valley), 94, 101 (Lillis Ranch).

A single specimen representing this subspecies was recognized by Dr. Merriam in the collections from loc. 1817. It somewhat resembles *T. buwaldana* Dickerson, but may be distinguished by its smaller size, narrower apical angle, and numerous fine ribs. It appears to be confined to, and be diagnostic of, the Capay stage, having been also found in the Capay Valley, at Marysville Buttes, and in the Oregon strata correlated with the Capay stage.

Turritella uvasana Conrad NEW SUBSPECIES Merriam MS.

Turritella uvasana "Gabb"; Cooper in Watts (1894) 57, 62 (San Joaquin Coal Mine and north of Los Gatos Creek).—Watts in Anderson (1908) 15 (north of Los Gatos Creek).—Anderson (1908) 15 (Oil City and Domengine Ranch).
Turritella uvasana Conrad; Arnold (1909) 14. *pl. 4, f. 11* (north of McLure Valley, near San Joaquin Coal Mine, Los Gatos Creek, and Domengine's Ranch).—Arnold & Anderson (1910) 71. *pl. 26, f. 11* (north of McLure Valley, near San Joaquin Coal Mine, Los Gatos Creek, and Domengine's Ranch).—Dickerson (1916) 434, 452 (between Domengine and Cantua creeks) (in part) (not *pl. 42, f. 6*).
Turritella applini Hanna; Clark in M. A. Hanna (1927) 260 (Coalinga).

Family VERMITIDAE

Genus SPIROGLYPHUS Daudin 1800

GENOTYPE (by subsequent designation, ? Grant & Gale 1931): *Spiroglyphus annulatus* Daudin. Recent, West Indies.

Typical *Spiroglyphus* is an attached shell, commonly being partially submerged in the shell of some larger species. The Eocene form was free, in the adult at least, although there is some evidence furnished by the irregularity of coiling in the early stages indicating attachment at that period.

Spiroglyphus (?) tejonensis Arnold

PLATE 20, FIGURES 20, 21, 22

Spiroglyphus ? tejonensis Arnold (1909) 14, 51. *pl. 4, f. 18* (described, Little Tar Canyon).—Arnold & Anderson (1910) 71. *pl. 26, f. 18* (Little Tar Canyon). Not *Spiroglyphus tejonensis* Arnold; Anderson in Dumble (1912) 32 (Salt Creek), nor *Spiroglyphus (?) tejonensis* Arnold; Dickerson (1916) *pl. 37, f. 5 a, b* = *Tornia* (?).—Clark (1921) 159 ("Meganos" north of Coalinga).

Hypotype 15835; loc. 7154; diameter 10.4 mm.
Hypotype 15836; loc. 7154; diameter 8.7 mm.
Hypotype 15837; loc. 7154; diameter 8.5 mm.

Arnold's type does not appear to be representative of the ordinary forms in this very variable species. The original description mentions but a single prominent revolving sulcation near the suture on the top of the whorl, and a circular cross-section to the whorl. The ordinary forms are inclined to be hexagonal in section, with a prominent sulca-

tion on either side of a prominent median ridge on both top and bottom of the whorl, and with 2 minor sulcations on the outer edge.

It if proves necessary to separate these from Arnold's species, the name *Spiroglyphus. capayensis* Merriam & Turner may be available, although that form seems to differ in the nature of the coiling, in which the body-whorl tends to "ride over" the preceding whorl.

The records of the occurrence of this species in the collections from Salt Creek (Arroyo Hondo formation, lower zone) appear to be based upon a small tubicolous annelid. It is present, however, in the upper zone of that formation near Domengine Creek.

Family ARCHITECTONICIDAE

Genus ARCHITECTONICA (Bolten) Roeding 1798

GENOTYPE (by subsequent designation, Gray 1847): *Trochus perspectivus* Linnaeus. Recent, Indo-Pacific.

Subgenus STELLAXIS Dall 1892

TYPE SPECIES (by original designation): *Solarium alveatum* Conrad. Claiborne and Jackson formations, Eocene, Gulf Coast of America.

Architectonica (Stellaxis) cognata Gabb

Architectonica cognata Gabb (1864) 117, *pl. 20, f. 72, a, c* (described, Martinez & Clayton).—Harris (1893) 97 (said to be *Solarium alveatum* Conrad).—Clark (1926) 115 (Coalinga).
Architectonica hornii Gabb; Dickerson (1916) 432, 448 (in part) (loc. 672).
? *Architectonica horni* Gabb; Anderson (1905) 164 (Avenal sandstones).
Solarium "cognata" Gabb; Dall (1892) 327 (belongs near *Stellaxis*).
Architectonica (Stellaxis) cognata Gabb; Stewart (1927) 343. *pl. 28, f. 7, 8* (lectotype and synonymy).

This appears to be a characteristic Domengine species, occurring in this horizon at Coalinga, Simi Valley, Martinez, and in Oregon. It has not been reported from the La Jolla formation at San Diego, nor from the Capay nor the Tejon horizons. A form which is at least subspecifically distinct occurs in the Arroyo Hondo formation at loc. 1817; the umbilical carina is almost smooth and the spiral line below the keel is not present.

It is difficult to reconcile Stewart's statement that the original figure is evidently based upon a number of specimens with Gabb's statement that "It is most abundant at Bull's Head Point, near Martinez, . . . where I found the individual figured." The writer is of the opinion that an undoubted holotype may yet be found.

The material identified by Dickerson as *A. hornii* Gabb from locality 672 has been examined by the writer, and should certainly be referred to *A. cognata.* Anderson's record of *A. horni* from the Avenal sand-

stones probably also is a misidentification of this species, but the occurrence of a single poorly preserved specimen of a new species which possesses a large number of spiral threads on the base of the whorl near the umbilicus, rather than the 2 threads in *A. hornii*, has resulted in questioning the reference of Anderson's identification to *A. cognata*. *A. hornii* Gabb* has so far been reliably reported only from the Tejon horizon.

Family LITTORINIDAE

Genus TECTARIUS Valenciennes 1833

GENOTYPE: *Trochus pagodus* Linnaeus. Recent, Indo-Pacific.

Valenciennes' original publication of this name† has not been available and the method by which the type is fixed is not known. However, the above-named species is cited as type by subsequent writers.

Tectarius ligniticus NEW SPECIES

PLATE 21, FIGURES 1, 3, 4

Holotype 15838; loc. 7005 (Simi Valley, California); length 23.3 mm., diameter 14.4 mm.
Hypotype 15839; loc. 7155; length 8.6 mm., diameter 7.3 mm.

DESCRIPTION.—Shell turbinate, heavy, imperforate, of 6 convex whorls marked by axial and spiral sculpturing; axial sculpturing consisting of strong, swollen, varix-like ribs, 8 on the penultimate and 7 on the ultimate whorl, extending from the suture to the periphery, but not present on the base of the whorls; spiral sculpturing of numerous primary and secondary threads, the primary threads between the suture and the periphery of the body-whorl 7, swollen and strongly developed where crossing the axials, and in the spaces between the axials 2 or 3 (generally 3) prominent nodes, the secondary ribbing also noded; base of the body-whorl marked by 7 primary and an equal number of secondary noded spirals; suture appressed, irregular, the succeeding whorl "riding" higher on the preceding whorl at each axial rib, and retreating in the interspaces; aperture subcircular; outer lip thick, retreating anteriorly, strongly lirate within and rounded anteriorly; columella calloused, subdentate at the base.

COMPARISON.—So far as the writer is aware, this is the first Eocene species of this genus to be described. It differs from *Tectarius pagodus* (Linnaeus), the genotype species, in possessing strong axial sculpturing and in lacking the carinate spiral sculpturing which develops the

---

* Gabb (1864) 117. *pl. 29, f. 224, 224 a.*
† Valenciennes (1833) 271.

strongly angulate carina. When more material is available, it may prove necessary to separate it subgenerically from the typical *Tectarius*.

This species may be *Calliostoma lignitica* Cooper,* which was described from a fragment, lacking the body-whorl, from the San Joaquin Coal Mine. That species, however, was said to possess 20 vertical ribs and only 3 strong revolving ribs, while the upper surface of the whorl was "nearly flat with a peripheral right angle from which the side of the whorl drops vertically." It would appear to be a distinct form, although nothing similar is in the collections from that locality.

Family CREPIDULIDAE

Genus CREPIDULA Lamarck 1799

GENOTYPE (by monotypy): *Patella fornicata* Lamarck. Recent, Atlantic and Gulf Coasts of the United States.

Subgenus SPIROCRYPTA Gabb 1864

TYPE SPECIES (by monotypy): *Crypta (Spirocrypta) pileum* Gabb. Eocene, Tejon formation, California.

Gabb formed this subgenus to receive his species, *C. pileum*, which possesses a peculiar upcurving of the posterior edge of the septa to form an open groove-like spiral from the septa upward toward the apex of the shell. He considered that this character indicated a stage of development intermediate between "*Trochita*" and "*Galerus*" and the typical "*Crypta*" (= *Crepidula*). *Trochita comma-nota* Adams from New Zealand appears to be a Recent representative of this group.

Crepidula (Spirocrypta) inornata Dickerson

PLATE 21, FIGURES 10, 11

Spirocrypta pileum Gabb (1869) 228 (New Idria). Not *Crypta pileum* Gabb 1864.
Crepidula inornata Dickerson (1916) 432, 489. *pl. 38, f. 5 a, b* (described, loc. 672).—Anderson & Hanna (1925) 122 (not at Tejon).—Clark (1926) 115 (Coalinga).
Crepidula tejonensis Dickerson (1916) 448 (nomen nudum).
Crepidula pileum (Gabb); Stewart (1927) 341. *pl. 29, f. 2, 3* (lectotype and synonymy).

Holotype 11804; loc. 672; length 8.3 mm., diameter 7.0 mm., height above base 4.0 mm.
Topotype 15841; loc. 672; length (incomplete) 5.5 mm., diameter 6.5 mm., height above base 3.7 mm.

Stewart (*op. cit.*) considered *Crepidula inornata* Dickerson and *C. dickersoni* Weaver & Palmer† synonymous with *C. pileum* (Gabb).‡ The Domengine species differs from *C. pileum* in being of smaller size,

* Cooper (1896) 331. *pl. 47, f. 5.*
† Weaver & Palmer (1922) 31. *pl. 11, f. 2; pl. 12, f. 9.*
‡ Gabb (1864) 137. *pl. 29, f. 233, a, b;* as *Crypta pileum.*

in possessing a spire which is higher on the shell and in which the penultimate whorl is rather bulbous and inflated and the earlier whorl is coiled in a plane. The spire of *C. pileum* is submarginal, and the penultimate whorl is not so inflated, resulting in the development of a lower apex. The spire of *C. inornata*, being higher and further removed from the margin of the shell, has resulted in the development of a funnel-like process due to the upward curving of the posterior portion of the septa. In *C. pileum* this curved area resembles a spiral groove rather than a funnel.

Specimens of *C. dickersoni* from the Cowlitz Formation show no trace of the upward curve on the septa and appear to belong to *Crepidula* (*sensu stricto*).

Family CALYPTRAEIDAE

Genus CALYPTRAEA Lamarck 1799

GENOTYPE (by monotypy): *Patella chinensis* Linnaeus. Recent, seas of Europe.

Calyptraea diegoana (Conrad)

Trochita diegoana Conrad (1855) 7, 17.—Conrad (1858) 327. *pl. 5, f. 42* (described, San Diego).
Galerus excentricus Gabb (1864) 136. *pl. 20, f. 95; pl. 29, f. 232, a* (described, Martinez, Clayton's, San Diego, and Tejon).—Cooper in Watts (1894) 57 (San Joaquin and California Coal Mines).—Stanton (1896) 1027 (New Idria).—Anderson (1905) 166 (coal mines).—Arnold (1909) 14. *pl. 4, f. 8* (several localities north and west of Coalinga).—Arnold & Anderson (1910) 71. *pl. 26, f. 8* (several localities north and west of Coalinga).
Calyptraea diegoana Conrad; Dall (1892) 353 (Miocene of California).—Stewart (1927) 340. *pl. 27, f. 15* (synonymy).—Merriam & Turner (1937) 99 (loc. 1817).
Calyptraea excentrica (Gabb); Dickerson (1916), 426, 427, 432, 449 (between Domengine and Cantua creeks).—Clark (1921) 158 ("Meganos" north of Coalinga).—Clark in M. A. Hanna (1927) 260 (Coalinga).
Calyptraea (*Galerus*) *calabasasensis* Nelson (1925) 419. *pl. 54, f. 8 a, b* (described, Martinez horizon, Simi Valley).
Calyptraea excentrica calabasensis (Nelson); Clark (1926) 115 (Coalinga).
? *Calyptraea washingtonensis* Weaver (1916) 44. *pl. 3, f. 44* (described, Lincoln horizon, Oligocene, Washington).

The range of variation in this species is very great, and it does not seem practicable to separate the forms mentioned in the synonymy above. There does seem to be a trend in the mean of variation through time, ranging from the forms with the round outline and high central apex (named *C. calabasasensis* by Nelson) in the Martinez horizon to those forms with the more oval outline and eccentrically placed spire in the Tejon, the Cowlitz, and the several Oligocene horizons. Both types are so intergraded in the Domengine material at hand as to make a separation impossible, although the *calabasasensis* type is predominant.

Family XENOPHORIDAE

Genus XENOPHORA Fischer de Waldheim 1807

GENOTYPE (by subsequent designation, Gray 1847): *Trochus conchyliophorus* Born (renamed *Xenophora laevigata* by Fischer de Waldheim). Recent, West Indies.

Xenophora NEW SPECIES

PLATE 21, FIGURE 7

Xenophora stockii Dickerson; Clark (1926) 116 (Coalinga).

Figured specimen 15842; loc. A-1165; length 6.3 mm., diameter 9.8 mm.

Small, probably immature, specimens of a new species of *Xenophora* occur in the collections from localities 2293 and A-1165. They differ from *X. stocki* Dickerson* in lacking the median shoulder on the whorl, and there is no evidence of nodes ornamenting the shell. The portions of the shell remaining suggest that the animal attached shell-fragments only.

Family NATICIDAE

Genus NATICA Scopoli 1777

GENOTYPE (by subsequent designation, Harris 1897): *Nerita vitellus* Linnaeus ("*Natica rufa* Born" of authors). Recent, West Pacific.

Natica domenginica NEW SPECIES

PLATE 21, FIGURES 5, 8

Natica uvasana Gabb; Dickerson (1916) 433, 451 (in part), (loc. 672) (not *pl. 38, f. 8*).

Holotype 15843; loc. 672; length 6.8 mm., diameter 7.0 mm.
Paratype 15844; loc. 672; length 3.2 mm., diameter 3.4 mm.

DESCRIPTION.—Shell small, thin, smooth, globose, with 4 post-nuclear whorls; spire moderately elevated, with sutures abutting; whorls ovate, with a definite shoulder and regularly rounded sides; umbilical region moderately large with a well-developed funicle spiraling into the funnel; an umbilical limb, distally defined by a low ridge, terminating at the anterior end of the aperture, and causing a subangulation of the aperture at this point; aperture semilunar, acutely angulate posteriorly and slightly angulate anteriorly; outer lip simple; inner lip with a small, thin parietal callus spreading out on the body-whorl and separated from the funicle by a definite sulcus.

COMPARISON.—*N. domenginica* differs from *N. uvasana* Gabb,† with which it has been confused, in possessing angulately shouldered

* Dickerson (1916) 502. *pl. 37, f. 4 a, b.*
† Gabb (1864) 212. *pl. 32, f. 277.*

whorls, a relatively higher spire, a smaller umbilical region with a relatively smaller funicle. The whorls are generally less inflated, and the ridge defining the limb of the umbilicus more pronounced on *N. uvasana*. *N. clementensis* M. A. Hanna possesses a deeply channeled suture.

Natica clementensis M. A. Hanna

Natica clementensis M. A. Hanna (1927) 304. *pl.. 47, f. 1, 3, 4, 6* (described, La Jolla formation, San Diego).

This small species of *Natica* is abundantly represented in the collections from locality A-1164. It may be recognized by the deeply channeled suture, the open umbilicus, and the absence of a funicle.

Genus POLINICES Montfort 1810

GENOTYPE (by original designation): *Polinices albus* Montfort = *Natica mammillaris* Lamarck = *Natica brunnea* Link. Recent, West Indies.

Polinices (Polinices) gesteri (Dickerson)

PLATE 21, FIGURES 2, 6

Natica gesteri Dickerson (1916) 426, 433, 451, 496. *pl. 38, f. 6* (described, loc. 1817).—Clark (1921) 159 ("Meganos" north of Coalinga).
Polinices gesteri (Dickerson); Clark (1926) 116 (Coalinga).
Polinices (Euspira) gesteri Dickerson; Clark & Woodford (1927) 121 (described from Meganos north of Coalinga; present in the Domengine).

Hypotype 15845; loc. 672; length (incomplete) 6.5 mm., diameter 5.0 mm.
Hypotype 15846; loc. 672; length 5.0 mm., diameter 4.0 mm.

Subgenus EUSPIRA Agassiz 1839

TYPE SPECIES (by subsequent designation, Dall 1915?): *Natica glaucinoides* Sowerby, not Deshayes. Eocene, England.

Polinices (Euspira) nuciformis (Gabb)

PLATE 21, FIGURES 12, 13, 14

Lunatia nuciformis Gabb (1864) 107. *pl. 28, f. 218* (described, Tejon).—Dickerson (1916) 426, 427, 433, 450 (loc. 1817); *pl. 39, f. 4* (Oroville).
Neverita nuciformis (Gabb); Dickerson (1914b) 115 (Oregon).
Natica nuciformis (Gabb); Anderson & Hanna (1925) 116. *pl. 10, f. 8* (Tejon).—Clark in M. A. Hanna (1927) 260 (Coalinga).
Polinices nuciformis (Gabb); Clark (1926) 116 (Coalinga).
Euspira nuciformis (Gabb); Stewart (1927) 323. *pl. 30, f. 16* (lectotype and synonymy).—Merriam & Turner (1937) 100 (loc. 1817).
Lunatia cowlitzensis Dickerson (1915) 57. *pl. 4, f. 12 a, b* (described, Cowlitz formation, Washington).

Hypotype 15847; loc. A-1016; length 17.3 mm., diameter 17.6 mm.
Hypotype 15848; loc. A-1165; length 14.1 mm., diameter 16.1 mm.
Hypotype 15849; loc. A-1165; length 16.0 mm., diameter 16.0 mm.

Genus NEVERITA Risso 1826

GENOTYPE (by monotypy): *Neverita josephinia* Risso. Recent, Mediterranean Sea?

Neverita globosa Gabb

PLATE 21, FIGURES 9, 15, 16, 17, 18, 19

Neverita globosa Gabb (1869) 161, 222. *pl. 27, f. 39* (described, "10 miles W. of Griswold's").—Turner & Stanton (1894) 95 (New Idria).—Stanton (1896) 1027 (New Idria).—Anderson (1905) 164, 166 (Avenal sandstones, and coal mines).—Turner in Anderson (1908) 10 (New Idria).—Anderson in Arnold (1909) 14 (southeast of Big Tar Canyon, and coal mines).—Anderson in Arnold & Anderson (1910) 72 (southeast of Big Tar Canyon, and coal mines).—Anderson in Dumble (1912) 32 (Salt Creek).—Dickerson (1916) 451 ("10 miles west of Griswold's, southeast of the sheep well on the road from San Juan to New Idria, Gabb").—Stewart (1927) 326. *pl. 28, f. 6* (holotype and synonymy).—Clark & Woodford (1927) 121, 122. *pl. 22, f. 5–10* (New Idria, San Benito County).—Turner (1938) 89. *pl. 19, f. 6, 7, 13–15* (occurs at New Idria, etc.).

Lunatia "hornii Gabb"; Arnold (1909) 14. *pl. 4, f. 9* (San Joaquin Coal Mine).—Arnold & Anderson (1910) 71. *pl. 26, f. 9* (San Joaquin Coal Mine).

? *Polinices globosa* Arnold & Hannibal (1913) 572 (Crescent formation, Washington).

Natica fiasco Hanna (1924) 173, 174 (new name for *Neverita globosa* Gabb, not *Natica globosa* King (1831) 344).—Anderson & Hanna (1925) 117 (not at Tejon).

Hypotype 15850; loc. A-1020; length 15.4 mm., diameter 14.9 mm.
Hypotype 15851; loc. A-1020; length 15.0 mm., diameter 14.3 mm.
Hypotype 15852; loc. A-1020; length 12.3 mm., diameter (incomplete) 11.7 mm.
Hypotype 15853; loc. A-1020; length 14.7 mm., diameter (incomplete) 14.2 mm.
Hypotype 15854; loc. 7155; length 11.0 mm., diameter 10.7 mm.

The type of this species came from the Domengine strata at the western end of the Vallecitos syncline. It was a very poorly preserved specimen, and all the topotype material in the collections has the same unfortunate defect. To illustrate the species, therefore, well-preserved material from the eastern end of the Vallecitos has been chosen.

The range of variation is very great, and the presence of the shoulder on the whorl is not a diagnostic character. The umbilical callus lacks the sulcation exhibited by *Neverita secta* Gabb, and in the typical form it does not entirely cover the umbilicus.

Hypotype 15854 shows the original color-pattern.

Neverita globosa Gabb reefensis NEW SUBSPECIES

PLATE 21, FIGURES 24, 25

Holotype 15855; loc. A-819; length 21.3 mm., diameter 21.2 mm.

This subspecies is distinguished from typical *N. globosa* Gabb by its general larger size and by the umbilical callus completely covering the umbilicus. It is rare in the Domengine horizon, where it is associated with the typical *N. globosa*, and an examination of collections from the Meganos and Capay stages has failed to reveal its occurrence.

Genus SINUM (Bolten) Roeding 1798

GENOTYPE (by subsequent designation, Dall 1915): *Helix haliotoides* Linnaeus. Recent, West Pacific ?.

Sinum obliquum (Gabb)

Naticina obliqua Gabb (1864) 109. *pl. 21, f. 112* (described, Martinez and Tejon).—Dickerson (1916) 427, 433, 450 (in part) (between Domengine and Cantua creeks).
Sinum obliquum (Gabb); Stewart (1927) 327. *pl. 30, f. 7 a* (lectotype and synonymy).
Sinum occidentis Weaver & Palmer (1922) 32. *pl. 11, f. 8, 26* (described, Cowlitz formation, Washington).
Sinum coryliforme Anderson & Hanna (1925) 120. *pl. 9, f. 10; pl. 10, f. 15; pl. 15, f. 8* (described, Tejon).

This species is not common in the Domengine collections, but rather abundant at loc. 1817 in the Arroyo Hondo formation.

Sigaretus costatus Cooper,* described from the San Joaquin Coal Mine, does not occur in our collections from that locality. The type is lost and the original figure is too poor to permit identification. Until topotype material is available the name must remain a *nomen dubium.* The presence of but 18 concentric ribs would seem to distinguish it from *Sinum obliquum.*

Family AMPULLOSPIRIDAE

Genus AMPULLELLA Cox 1931†

Genotype (by original designation): *Ampullaria depressa* Lamarck. Eocene, Paris Basin, France.

This genus is the *Ampullina* Bowdich‡ of authors. Bowdich, however, merely attached the name to a poor figure which was identified by Dall as representing *Ampullaria depressa* Lamarck. According to Cox§ "It cannot possibly represent the Eocene species '*Ampullaria*' *depressa* Lamarck, . . . since it portrays a specimen with an open umbilicus, differing absolutely in appearance from that species . . . I am of the opinion that the species depicted is *Natica labellata* Lamarck."

Ampullella (Ampullella) schencki new species

Plate 21, figures 20, 21, 26

Holotype 15856; loc. 4170; length (incomplete) 20.8 mm., diameter 18.2 mm.
Paratype 15857; loc. 4170; length (incomplete) 15.3 mm., diameter 15.7 mm.
Paratype 15858; loc. 4170; length (incomplete) 17.2 mm., diameter 17.5 mm.

Description.—Shell of medium size, globose, ornamented with microscopic spiral threads; spire moderately high, the whorls 6, rounded with a slight shoulder, the suture channeled; aperture semi-

* Cooper (1896) 332. *pl. 47, f. 6.*
† Cox (1931) 38, 41.
‡ Bowdich (1822) 31. *pl. 9, f. 2.*
§ Cox (1930) 170.

lunar, angulate posteriorly, rounded anteriorly, extending to the median axis of the shell; outer lip simple, thickened at the anterior end, where slightly recurved; inner lip calloused, the callus slightly inside the recurved anterior end of the lip, forming a small pseudo-umbilicus between the callus and the lip.

COMPARISON.—*Ampullella schencki* is the first species of *Ampullella* (*sensu stricto*) to be described from the West Coast Eocene. It may be distinguished from all other described species by the slightly recurved outer lip and the pseudo-umbilicus formed between the callus and the lip. The fine spiral sculpturing will also distinguish this species.

Named in honor of Dr. H. G. Schenck, of Stanford University.

Genus CROMMIUM Cossman 1888

GENOTYPE (by original designation): *Ampullina willemati* Deshayes. Eocene, Paris Basin, France.

Crommium andersoni (Dickerson)

PLATE 21, FIGURES 22, 23

Gyrodes dowelli "White;" Cooper in Watts (1894) 57 (California Coal Mine).
? *Lunatia* "*horni* Gabb;" Anderson (1905) 166 (coal mines).
Lunatia sp. a Arnold (1909) 14. *pl. 4, f. 13* (San Joaquin Coal Mine).—Arnold & Anderson (1910) 71. *pl. 26, f. 13* (San Joaquin Coal Mine).
Amauropsis andersoni Dickerson (1914b) 120. *pl. 12, f. 2a, b* (described, Oregon).
Amauropsis umpquaensis Dickerson (1914b) 120. *pl. 12, f. 3 a, b* (described, Oregon).
Ampullina andersoni (Dickerson); Anderson & Hanna (1925) 118 (not at Tejon).
Ampullina (*Crommium*) *andersoni* (Dickerson). Turner (1938) 87. *pl. 19, f. 1, 2, 4, 5* (Oregon).

Hypotype 15859; loc. A-1154; length 17.0 mm., diameter 16.8 mm.
Hypotype 15860; loc. A-1154; length 17.4 mm., diameter 16.8 mm.

The inner lip of this species is angulate anteriorly, the angulation being reflected in the development of a ridge which spirals into the open umbilicus. The ridge is possibly more strongly developed upon the specimens from the Coalinga district than on the specimens from the Oregon type locality, but otherwise the representatives from the two areas agree. Only the "low-spired form" represented by Dickerson's originally described *Amauropsis andersoni* occurs in the collections. The high-spired type, represented by "*Amauropsis umpquaensis*," is not found.

Genus CERNINA Gray 1840

GENOTYPE (by original designation): *Natica fluctuata* G. B. Sowerby. Recent, South Pacific.

Subgenus EOCERNINA Gardner & Bowles 1934*

TYPE SPECIES (by original designation): *Natica hannibali* ("*hannabali*") Dickerson. Middle Eocene (Umpqua formation), Oregon.

* Gardner & Bowles (1934) 243.

Cernina (Eocernina) hannibali (Dickerson)

PLATE 22, FIGURES 1, 3

Amauropsis oviformis ? Gabb; Arnold (1909) 13. *pl. 4, f. 7* (Reef Ridge).—Arnold & Anderson (1910) 71. *pl. 26, f. 7* (Reef Ridge).
Natica hannibali Dickerson (1914b) 119. *pl. 12, f. 5 a, b* (described, Oregon).—Dickerson (1916) 433, 451. *pl. 38, f. 9 a, b* (between Domengine and Cantua creeks).—Clark (1921) 159 ("Meganos" north of Coalinga).
Natica (Cryptonatica) hannibali Waring (1917) *pl. 15, f. 21, 22, 23* (Calabasas Area).
Ampullina hannibali (Dickerson); Anderson & Hanna (1925) 118 (not at Tejon, present at Salt Creek, Fresno County).—Clark (1926) 115 (Coalinga).
Globularia hannibali (Dickerson); Stewart (1927) 331 (very common in the Domengine horizon).
Cernina (Eocernina) hannibali ("*hannabali*") (Dickerson); Gardner & Bowles (1934) 243 (type species of *Eocernina*).

Hypotype 15861; loc. 3296 (Llajas formation); length 56.7 mm., maximum diameter 46.5 mm.

This species occurs in the upper zone of the Arroyo Hondo formation and in the Domengine formation in the Coalinga area.

Genus AMAURELLINA Bayle; Fischer 1885

GENOTYPE (by monotypy): *Amaurellina spirata* (Lamarck). Eocene, Paris Basin, France.

Amaurellina caleocia NEW SPECIES

PLATE 22, FIGURES 4, 5, 6

Amauropsis alveata (Conrad); Dickerson (1916) 432 (in part), 448 (in part). *pl. 38, f. 7* (between Domengine and Cantua creeks).
? *Amauropsis alveata* Gabb; Anderson (1908) 15 (near Domengine's Ranch).
Amaurellina moragai lajollaensis Stewart (1927) 336 (in part, Coalinga records) not *pl. 28, f. 2*.

Holotype 33781; loc. 672; length (incomplete) 15.0 mm., diameter 12.6 mm.
Paratype 15862; loc. 672; length 19.9 mm., diameter 16.4 mm.

DESCRIPTION.—Shell of medium size, moderately heavy, with about 6 whorls; spire high, the whorls angulate, but without a shoulder carina, the suture abutting, very slightly channeled; body-whorl globose, ornamented with spiral striae, each pair of striae generally having a weaker striation between; aperture somewhat biangulate posteriorly; outer lip sharp, recurved anteriorly to form a well-developed siphonal fasciole, and excavated to form a broad, shallow notch; inner lip with a thin callus; umbilicus wide, a funicle-like ridge ascending from the siphonal fasciole.

COMPARISON.—*A. caleocia* resembles *A. moragai lajollaensis* Stewart* in the presence of spiral striae on the whorls. In that species, however, the striae tend to be of equal strength, and are generally rather equally spaced over the surface of the whorl. The Coalinga

---

* Stewart (1927) 336. *pl. 28, f. 2*.

specimens also differ from Stewart's subspecies in possessing a lower spire, with more rounded shoulders to the whorls which lack all trace of a carina; the body-whorl is more globose, and shorter in proportion to the diameter; the aperture possesses a shallow, broad notch; the siphonal fasciole is more strongly developed; the umbilicus is widely open, rather than almost closed, and possesses a funicle-like ridge which is not developed on the type of *A. moragai lajollaensis*. *A. caleocia* may be separated from *A. moragai* Stewart* by the absence of the strong carina on the shoulder of the whorls.

Amaurellina garzaensis NEW SPECIES

PLATE 22, FIGURES 9, 12, 16

Holotype 15863; loc. A-1164; length 8.7 mm., diameter 6.9 mm.
Paratype 15864; loc. A-1164; length 10.9 mm., diameter 9.0 mm.
Paratype 15865; loc. A-1164; length (incomplete) 8.5 mm., diameter 7.2 mm.

DESCRIPTION.—Shell small, moderately heavy, of 5 whorls; spire moderately high, the sutures impressed, channeled; whorls globose, without a defined shoulder, marked by approximately equidistant, incised striae; aperture semilunar, angulate posteriorly, rounded anteriorly, the lip being there reflected to form a siphonal fasciole; inner lip callused; umbilicus small, almost closed by the callus and a well-defined funicle-like ridge from the siphonal fasciole; outer lip sharp, without a defined anterior notch.

COMPARISON.—This small species may be distinguished from all other described species of the genus by the absence of a defined shoulder on the whorls.

Amaurellina hendoni Turner

PLATE 22, FIGURES 7, 10

Amauropsis sp. Dickerson (1916) 426, 432 (loc. 672 in error), (loc. 1817).
Amauropsis alveata "(Conrad)"; Clark (1921) 158 ("Meganos" north of Coalinga).
Amaurellina hendoni Turner (1938) 86. *pl. 20, f. 7, 8, 11.*

Holotype 33630; Univ. Oregon loc. 139/12; length 23.8 mm.; diameter 20.2 mm.
Paratype 33178; loc. A-662; length 26.0 mm., diameter 20.0 mm.

A. hendoni may be distinguished from the most closely related form, *A. moragai lajollaensis* Stewart, by its less sharply angulate shoulder, more globose appearance, lack of prominent spiral ornamentation, and larger umbilicus.

Abundant poorly preserved specimens in the collections from loc.

* Stewart (1927) 334. *pl. 28, f. 3.*

1817 are similar in outline to *A. hendoni*, and occurring in an equivalent stratigraphic position, are tentatively referred to this species.

Amaurellina (?) multiangulata NEW SPECIES

PLATE 22, FIGURES 2, 8, 13

Holotype 15866; loc. A-1016; length 18.0 mm.; diameter 14.8 mm.
Paratype 15867; loc. A-1016; length (incomplete) 15.4 mm.; diameter 14.3 mm.
Paratype 15868; loc. A-1016; length (incomplete) 14.7 mm.; diameter 12.0 mm.

DESCRIPTION.—Shell of medium size, thin, of six whorls; spire high, the suture abutting, the early whorls rounded, the last 3 shouldered; body-whorl inflated; aperture ovate, biangulate posteriorly, rounded anteriorly; outer lip simple; inner lip with a thin callus on the whorl, and recurved anteriorly, the recurved lip almost closing the small umbilicus; surface of the whorl marked by a series of spiral ridges, these making the whorl appear to be formed by a series of small flattened ribbons in angulate relation to one another.

COMPARISON.—The angulate appearance of the sides of the body-whorl will at once distinguish this species from all other described forms.

The absence of a siphonal funicle would seem to separate this species from *Amaurellina* (*sensu stricto*). It probably belongs to an unnamed group, but due to the lack of sufficient comparative material it seems wiser to refer it to this genus at the present time.

Genus **PACHYCROMMIUM** Woodring 1928

GENOTYPE (by original designation): *Amaura guppyi* Gabb. Miocene, Dominican Republic.

According to Stewart* specimens of *Pachycrommium guppyi* from Santo Domingo have a fine spiral sculpture of punctate lines on the body-whorl, and similar but more widely spaced lines may be seen on *P. acuminatum* (Lamarck) (Eocene, Paris Basin). The value of such sculpture may be questioned as a generic character, but its entire absence on the California species "*Pachycrommium*" *clarki* (Stewart) seems to be significant. Furthermore, the specimens from Santo Domingo as figured by Woodring† and by Pilsbry‡ show a pointed anterior end to the aperture, which, judging from the figures, may have been a canal-like notch. A similar development may be seen on the outer edge of the anterior portion of the aperture of *P. acuminatum*

* Stewart (1930) 40.
† Woodring (1928) *pl. 31, f. 8.*
‡ Pilsbry (1922) *pl. 34, f. 25, 26, 27.*

as figured by Cossmann & Pissarro.* This notch is not present on the West Coast species.

The specimen figured by Woodring as *P. guppyi* from Bowden may be specifically distinct from the Santo Domingan form. The notch is not developed, the shell is more slender with a proportionally higher spire, lacks the shoulder on the whorl and appears to have a more globosely rounded body-whorl. Specimens in the collections of the University of California from Bowden (loc. S-2) fail to reveal any punctate spiral sculpturing.

Pachycrommium (?) clarki (Stewart)

PLATE 22, FIGURES 11, 30

Euspira alveata "(Conrad)"; Gabb (1869) 223 (Griswold's).
? *Amauropsis alveata* (Conrad); Turner & Stanton (1894) 95 (New Idria).—Stanton (1896) 1027 (New Idria).
? *Amauropsis alveata* Gabb; Anderson (1905) 164 (Avenal sandstones).—Turner in Anderson (1908) 10 (New Idria).
Amauropsis alveata "Conrad"; Arnold (1909) 13. *pl. 4, f. 21* (southwest of Domengine's Ranch).—Arnold & Anderson (1910) 71. *pl. 26, f. 21* (southwest of Domengine's Ranch).—Dickerson (1916) 432 (in part), 448 (in part) (between Domengine and Cantua creeks); not *pl. 38, f. 7*.
Amaurellina (Euspirocrommium) clarki Stewart (1927) 336–338. *pl. 26, f. 8, 9* (described, Llajas Canyon, Simi Valley).

Hypotype 15869; loc. A-1016; length (incomplete) 51.0 mm., diameter 39.0 mm.
Hypotype 15870; loc. A-1012; length (incomplete) 33.2 mm., diameter 23.5 mm.

Suborder PTENOGLOSSA

Family EPITONIIDAE

Genus ACRILLA H. Adams 1860

GENOTYPE (by original designation): *Acrilla acuminata* (H. & A. Adams). Recent, Phillippines.

Subgenus FERMINOSCALA Dall 1908

TYPE SPECIES (by original designation): *Acrilla ferminiana* (Dall). Recent, Gulf of Panama to California.

Acrilla (Ferminoscala) tejonensis (Dickerson)

PLATE 22, FIGURES 14, 18

Epitonium "tejonensis" Dickerson (1916) 433, 449, 491. *pl. 38, f. 4* (described, loc. 672).—Anderson & Hanna (1925) 124 (from loc. 672, Parson's Peak, Fresno County).—Clark (1926) 115 (Coalinga).
Acrilla (Ferminoscala) tejonensis (Dickerson); Durham (1937) 507.

Topotype 15881; loc. 672; length (incomplete) 7.6 mm., diameter 4.7 mm.
Topotype 15882; loc. 672; length (incomplete) 8.6 mm., diameter 5.5 mm.

* Cossmann & Pissarro (1911) *pl. 11, f. 64 bis 4*.

The type is poorly preserved and, as a result, the original description is inaccurate. Better preserved topotype material permits the following corrections: The varices are strongly developed, lamellar, and coronate on the shoulder, with no evidence of swelling in the middle of the whorl; there are but 7 spiral threads, which are visible only in the area between the varices and do not cross them, nor are the varices noded at the intersection; the aperture is round, with a well-developed umbilical opening between the inner lip and the base of the whorl, which is marked by a strong spiral at the angulation, with 2 or 3 weaker spirals between it and the umbilicus.

This species is at present known only from locality 672. The cast from Marysville Buttes mentioned by Dickerson is very poorly preserved, but there does not appear to have been any umbilicus, and the base of the body-whorl seems to have possessed only the spiral at the angulation.

Suborder GYMNOGLOSSA

Family PYRAMIDELLIDAE

Genus PYRAMIDELLA Lamarck 1799

GENOTYPE (by monotypy): *Turbo dolabratus* Linnaeus. Recent, West Indies.

Pyramidella cf. etheringtoni M. A. Hanna

Odostomia packi Dickerson (1916) 427, 433, 451 (loc. 1817).

The specimen identified by Dickerson as *Odostomia packi** agrees more closely with *Pyramidella etheringtoni* M. A. Hanna† in the apical angle and in general proportions of the whorls. "*Odostomia*" *packi* is a *Pyramidella*.

Genus ODOSTOMIA Fleming 1817

GENOTYPE: *Turbo plicatus* Montagu. Recent, Mediterranean Sea.

Cossmann‡ uses *Odontostomia* Jeffreys 1837, for this genus on the grounds that *Odostomia* Fleming, which he dates from 1819, was preoccupied by *Odostomia* Say 1817, a genus of *Pupidae*. Most authors have given Fleming's name as of 1817, but since the original publication is not available, the writer has preferred to follow established usage and use the name *Odostomia* for the following species.

---

* Dickerson (1916) 498. *pl. 37, f. 11* (described, Rose Canyon, San Diego County).
† M. A. Hanna (1927) 302. *pl. 46, f. 14, 18, 22* (described, La Jolla formation).
‡ Cossmann (1921) 236.

Odostomia griswoldensis NEW SPECIES

PLATE 22, FIGURES 15, 19

Holotype 15887; loc A-1154; length (incomplete) 3.2 mm., diameter 1.4 mm.
Paratype 15888; loc. A-1154; length (incomplete) 2.3 mm., diameter 1.2 mm.

DESCRIPTION.—Shell small, imperforate, turrited, of 5+ very gently convex, almost flat-sided whorls; nucleus missing; sutures appressed, linear; aperture long, narrow, sharply angulate posteriorly, subangulate at base with an indistinct anterior emargination; inner lip with a sharp columellar fold at the anterior third of the length of the aperture.

COMPARISON.—*O. griswoldensis* differs from previously described West American Eocene species in having sutures which are appressed and linear, rather than depressed or channeled. The aperture is narrower in proportion to the length and the subangulate basal lip with a well-developed fold on the anterior portion of the inner lip is also distinctive.

Family MELANELLIDAE

Genus MELANELLA Bowdich 1822

GENOTYPE (by monotypy): *Melanella dufresnii* Bowdich. Recent.

According to Grant & Gale,* Bowdich's figure shows one of the forms with the flexed or curved spire which Bartsch† placed in the subgeneric group *Balcis* Leach 1852. That name first appeared as *Balcis* Leach in Gray 1847‡, with the type stated to be *Helix subulata.* This species being the type of *Subularia* Monterosato, that genus must fall into synonymy of *Balcis* Leach.

Section EULIMA Risso 1826

TYPE SPECIES (*fide* Bartsch 1917): *Eulima elegantissima* Risso = *Melanella polita* (Linnaeus). Recent, seas of Europe.

The segregation of the straight and flexed types of *Melanella* is probably a wholly artificial arrangement, but until the two groups have been sufficiently studied to determine whether the flexed spire is a genetic character or simply a response to some environmental condition it seems best to distinguish between the two groups. This is the straight-shelled group (*Melanella, sensu stricto,* of Bartsch).

Risso's publication§ is not available, and the type citation is given as of Bartsch (*op. cit.*), who has monographed the group. Herrmann-

* Grant & Gale (1931) 861.
† Bartsch (1917) 302.
‡ Gray (1847b) 160.
§ Risso (1826) 123.

sen* cites *Turbo subulatus* Donovan as the type, while Gray† gives *Helix polita* for *Eulima* Risso, and *Helix subulata* for *Balcis* Leach MS. and *Eulima* sp. Risso. Herrmannsen's designation is the older, and if no type was designated by Risso, and no earlier subsequent designation is available, must stand, making *Eulima* the oldest name available for the forms known as *Subularia* Monterosato (= *Balcis* Leach; Gray).

Melanella coalingana NEW SPECIES

PLATE 22, FIGURE 17

Holotype 15873; loc. 1817; length (incomplete) 2.6 mm., diameter 1.0 mm.

DESCRIPTION.—Shell small, straight, smooth, polished, the apical angle twelve degrees; number of whorls unknown, about three and one half on the holotype; suture slightly impressed; whorls of spire gently convex above the suture; body-whorl produced, with inner lip appressed to it for its entire length; outer lip thin; posterior angle of aperture sharply acute; base rounded; parietal wall calloused.

COMPARISON.—*M. coalingana* differs from *M. acuella* Anderson & Hanna,‡ the only other described western Eocene form, in having a smaller apical angle (twenty-two degrees in *M. acuella*), a slightly impressed suture, and a callus on the parietal wall. The figure of *M. acuella* suggests that this form may be one of the flexed types referred by Bartsch to the subgenus *Balcis* Leach (= *Melanella, sensu stricto*, according to Grant & Gale).

Genus NISO Risso 1826

GENOTYPE (by monotypy): *Niso eburnea* Risso. Recent, Mediterranean Sea.

Niso polita Gabb

Niso polita Gabb (1864) 116. *pl. 21, f. 113* (described, Martinez).—Stewart (1927) 320. *pl. 27, f. 1; text-f. 2* (lectotype and synonymy).

This species was described from deposits of Domengine age from near Martinez, and is present in the Capay horizon at Marysville Buttes.§ The record of its occurrence in the Martinez horizon¶ appears to be based upon two specimens in the State Survey Collection, labelled as this species, from Martinez. One, which is not this species, is in the brown sandstone matrix which is characteristic of the Martinez

* Herrmannsen (1847) 431. (April.)
† Gray (1847b) 160. (November.)
‡ Anderson & Hanna (1925) 131. *pl. 14, f. 1.*
§ Dickerson (1913) 264, 270 ("*polito*" in error).—See also Dickerson (1916) 408, 450.
¶ Dickerson (1914a) 110, 113 ("*polito*" in error).—See also Dickerson (1916) 450, 454.

horizon at this locality; the other, which is correctly determined, is in a hard, gray, limy sandstone full of shell-fragments and appears to have come from the Domengine horizon.

Order SCUTIBRANCHIATA

Suborder RHIPIDOGLOSSA

Family TURBINIDAE

Genus HOMALOPOMA Carpenter 1864

Genotype (by monotypy): *Turbo sanguineus* Linnaeus. Recent, Mediterranean and Adriatic Seas.

Homalopoma wattsi (Dickerson)

Plate 22, figures 21, 22

Monodonta wattsi Dickerson (1916) 494. *pl. 40, f. 3 a, b* (described, Marysville Buttes).
Monodonta "wasti Dickerson;" Cossmann (1916) 110 ("probably *Monilea*").
? *Margaritella angulata ?* Gabb; Anderson in Dumble (1912) 32 (Salt Creek).
Homalopoma wattsi (Dickerson); Merriam & Turner (1937) 100 (Lillis Ranch).

Hypotype 15871; loc. 1817; length 5.5 mm., diameter 7.5 mm.

This species appears to be characteristic of the Capay stage, occurring in that zone at Marysville Buttes, the type locality for the species, in the type Capay, and in Oregon, as well as at Coalinga. The Coalinga specimens tend to have a slightly lower spire than the more northern forms, but otherwise are identical.

There are two teeth on the inner edge of the basal lip, the one near the columella being the larger. No suggestion of the great tooth-development of *Monodonta labio*, the monotype species of *Monodonta*, is to be seen. The lack of an open umbilicus invalidates Cossmann's suggestion that this species is probably a *Monilea.*

Homalopoma umpquaensis Merriam & Turner domenginensis
NEW SUBSPECIES

Plate 22, figure 27

Holotype 15872; loc. 672; length 4.2 mm., diameter 4.7 mm.

Description.—Shell small, turbinate, of 2 smooth rounded nuclear and 3 flat-sided post-nuclear whorls; suture deeply channeled, distinct, the apertural portion of the body-whorl tending to turn slightly anteriorly causing an appreciable widening of the suture at that point; post-nuclear whorls ornamented by strong, rounded spiral cords, 6 on the penultimate whorl, the first and sixth being more strongly developed than the rest, and 9 on the body-whorl, the first, sixth and

ninth being most strongly developed; whorl so angulated at the sixth spiral that the last three are virtually on the base of the shell, which has 6 spirals upon it; aperture rounded, entire; outer lip retreating anteriorly; basal inner lip calloused, slightly flaring, with a small node; umbilicus closed.

COMPARISON.—*H. umpquaensis domenginensis*, although having the same number of whorls as *H. umpquaensis* Merriam & Turner,* is only approximately one half as large. On that species the seventh and eleventh spiral cords on the body-whorl are strongest, and the shell is angulated at the seventh spiral to form a flat-sided area that is approximately parallel to the axis of the shell. The Domengine species has a smaller number of spirals and is much more strongly angulated at the sixth rib so that a flat portion of the whorl is not developed. *H. wattsi* (Dickerson) possesses a small node on the base of the aperture in addition to the node at the corner of the basal inner lip, and the body-whorl on that species is rounded, not angulated.

Family NERITIDAE

Genus NERITA Linnaeus 1758

GENOTYPE (by subsequent designation, Montfort 1810): *Nerita peloronta* Linnaeus. Recent, Bermudas and Florida Keys to Venezuela.

It is unfortunate that Baker's recent study of the *Neritidae*,† based upon studies of the radula, should give so little attention to shell-characters as to be of little use to the paleontologist. The assignments here made are based upon the general similarities of outline, sculpture, and apertural features to recent species which were considered by Baker in his paper.

Subgenus AMPHINERITA von Martens 1887

TYPE SPECIES (by subsequent designation): *Nerita umlaasiana* Krauss. Natal.

According to Baker the specific distinction of *N. umlaasiana* Krauss from *N. polita* Linnaeus is very doubtful. The tentative assignment of the new species *Nerita eorex* to this section is based upon features of similarity with *N. polita*.

Nerita (Amphinerita) eorex NEW SPECIES

PLATE 22, FIGURES 24, 26, 29

Holotype 15874; loc. A-1165; length 9.3 mm., diameter 10.1 mm.
Paratype 15880; loc. A-1281; length 8.0 mm., diameter 9.5 mm.

---

* Merriam & Turner (1937) 104. *pl. 6, f. 6.*
† Baker (1923) 117–178. *pl. 9–16.*

DESCRIPTION.—Shell of medium size; spire very low, rising but slightly above the body-whorl; visible whorls 4; suture linear, inconspicuous; body-whorl large, inflated; aperture large; outer lip sharp; inner lip with heavy callus, slightly flattened, with 5 subequal, large denticles on the edge of the columellar lip; surface of shell smooth, marked only by lines of growth.

The preserved evidence indicates a variable color-pattern for this species. The holotype seems to have been a lighter (white or cream) color above with a wide median band of chestnut over most of the body-whorl. A specimen from loc. A-1281 was of an olive-green color with an irregular pattern of cream and yellow spots. Topotype material from loc. A-1165 shows a similar pattern, as well as a pattern composed of alternating bands of light and darker chestnut-color which are parallel with the lines of growth on the shell.

COMPARISON.—*Nerita eorex* is very similar to specimens of *N. polita* Linnaeus of comparable size, the shell being slightly longer in proportion to the diameter than is to be seen on the Recent species, and the denticles on the inner lip are of more uniform size.

This species, known only from the Reef Ridge section, is the only smooth-shelled *Nerita* from the West American Eocene.

Named for its occurrence in the Eocene of Kings County, California.

Subgenus THELIOSTYLA Mörch 1852

TYPE SPECIES (by subsequent designation): *Nerita albicilla* Linnaeus Recent, Africa to Tahiti, China to Australia.

The reference of *Nerita triangulata* Gabb to this section is based upon the presence of a tuberculate columellar area very similar to that observed upon the type species.

This is the *Nerita* (*sensu stricto*) of the authors who considered Lamarck's citation of *N. exuvia* as the example of *Nerita* a valid type designation. Since, by Opinion 79 of the International Committee of Zoological Nomenclature, Lamarck's examples are not valid citations, the first valid designation, that of Montfort 1810, who cited *N. peloronta*, fixes the genus *Nerita* and allows the use of Mörch's name for those species with strong spiral sculpture and a tuberculate columellar area.

Nerita is an ancient group and it is not surprising that recent sectional groups should be represented in the Eocene faunas.

Nerita (Theliostyla) triangulata Gabb

PLATE 22, FIGURES 31, 33, 34

Nerita (Theliostyla) triangulata Gabb (1869) 170. *pl. 28, f. 52, a* (described, New Idria).—Stanton (1896) 1027 (New Idria).
Nerita triangulata Gabb; Anderson (1905) 166 (coal mines) —Arnold (1909) 14. *pl. 4, f. 12, a* (San Joaquin Coal Mine).—Arnold & Anderson (1910) 71. *pl. 26, f. 12, a* (San Joaquin Coal Mine).—Dickerson (1916) 450 (near New Idria).—Clark (1926) 116 (Coalinga). —Stewart (1927) 291 (type material not found), 301 (from near New Idria).

Hypotype 15875; loc. 7155; length 7.3 mm., diameter 9.7 mm.
Hypotype 15876; loc 7155; length 4.2 mm., diameter 5.6 mm.

This, a brackish-water species, is rare at the type locality. Gabb mentions having only two specimens, and a single poorly preserved individual occurs in our collections. It is fairly abundant in the carbonaceous strata at the San Joaquin and California Coal Mines northwest of Coalinga.

Genus VELATES Montfort 1810

GENOTYPE (by original designation): *Velates conoideus* (Lamarck) = *Nerita perversa* Gmelin, *Nerita schmideliana sinistrorsa, fossilis* Chemnitz. Eocene, Paris Basin, France.

Velates perversus (Gmelin)

For a discussion of the occurrence of this species the reader is referred to an earlier paper by the writer.*

Velates californicus Vokes

Velates californicus Vokes (1935b) 384, 385. *pl. 26, f. 3–7* (described, Simi Valley and Coalinga).

Family TROCHIDAE

Subfamily GIBBULINAE

Genus CALLIOVARICA NEW GENUS

GENOTYPE: *Calliovarica eocensis* new species. Eocene, Capay Horizon, California.

The genus *Calliovarica* is erected to receive a new and unique species of trochid gastropod from the California Eocene. It may be characterized as follows:

Shell of medium size, conic, imperforate; inner part of shell nacreous; aperture oblique to vertical axis of shell, rounded; outer lip thickened, strongly reflected, represented on the earlier whorls by numerous well-developed varices.

The strongly reflected, thickened outer lip and the numerous varices separate this genus from the previously described *Calliostoma*-like genera.

* Vokes (1935b) 382, 383. *pl. 25, f. 1–5; pl. 26, f. 1, 2.*

Calliovarica eocensis NEW SPECIES

PLATE 22, FIGURES 20, 23, 25, 28

Holotype 15884; loc. 1817; length 19.1 mm., diameter 15.3 mm.
Paratype 15885; loc 1817; length (crushed) 17.5 mm., diameter (crushed) 15.3 mm.
Paratype 15886; loc 1817; length (incomplete) 11.9 mm., diameter 9.2 mm.

DESCRIPTION.—Shell of medium size, conic, imperforate, of approximately 8 whorls, angulate above and below the impressed sutures, and flat-sided between the angulations; lines of angulation marked by spiral rows of small nodes, with a third row between, slightly nearer the posterior angulation than the anterior; numerous fine, raised, obliquely axial ridges crossing the whorl, generally one on each side of each node; outer shell-layer generally missing, the inner layer nacreous, showing spiral nodes, but lacking the axial ribbing; whorls crossed by numerous varices extending from suture to suture; basal edge of the body-whorl angulate, marked by a spiral ridge; base sculptured by 5 low spiral ridges; aperture oblique, rounded; outer lip strongly reflected, thickened; inner lip calloused; columella slightly thickened, but not dentate.

COMPARISON.—No species similar to this has been previously described, and it may at once be distinguished from known *Trochidae* by the numerous varices, which are present on all specimens examined, as well as by the strongly reflected outer lip.

Suborder DOCOGLOSSA

Family ACMAEIDAE

Genus ACMAEA Eschscholtz in Kotzebue 1830

GENOTYPE (by subsequent designation, Dall 1871): *Acmaea mitra* "Eschscholtz" Rathke. Recent, Pacific coast of North America.

The genus *Acmaea* was first proposed in the appendix of volume 2 of the English translation of Kotzebue's "Neue Reise um die Welt in den Jahren 1823, 24, 25 und 26" without species named. The first publication of species referred to the genus was in Rathke 1833 ("Eschscholtz's Zool. Atlas" part 5), and it was from this list that Dall's type designation was made.

Acmaea NEW SPECIES

PLATE 22, FIGURE 32

Figured specimen 15883; loc. A-1164; length 3.5 mm., altitude 1.5 mm., width (incomplete) 2 3 mm.

A single poorly preserved specimen of a minute *Acmaea* occurs in the collections. The shell is conic, high, with the apex far anterior. The shell is broken at the apex, but there is no evidence that it was perforate. The surface is almost smooth with the exception of a few subobsolete ribs immediately under the apex.

Additional material is necessary before it will be possible to give an adequate diagnosis of the species.

FOSSIL LOCALITIES

Localities in the type section of the Domengine formation:

All localities are within the area included in the Coalinga Quadrangle.*

672 S. E. ¼ of N. W. ¼ of Sec. 24, T. 18 S., R. 14 E., massive sandstone forming southern portion of the crest of Parson's Peak. Locality is about 45 feet above base of the Domengine formation.

2286 N. E. corner of S. W. ¼ of N. E. ¼ of Sec. 9, T. 19 S., R. 15 E., elevation 1300 feet, in last side canyon to north. Coll. B. L. Clark.

2287 Western side of Domengine Canyon in S. W. corner of S. W. ¼ of S. E. ¼ of Sec. 29, T. 18 S., R. 15 E., elevation 1150 feet. Coll. B. L. Clark.

2289 N. E. corner of S. E. ¼ of S. E. ¼ of Sec. 32, T. 18 S., R. 15 E., elevation 1500 feet on hillside above wide open valley. Coll. B. L. Clark.

2290 On crest of ridge overlooking Domengine Creek, elevation 1300 feet. Coll. B. L. Clark.

2291 N. E. corner of S. E. ¼ of S. W. ¼ of Sec. 29, T. 18 S., R. 15 E., elevation 1200 feet, Coll. B. L. Clark.

2292 On hill in N. W. corner of N. E. ¼ of S. E. ¼ of Sec. 32, T. 18 S., R. 15 E., elevation 1700 feet. Coll. B. L. Clark.

3315 Base of Domengine formation immediately south of Domengine Creek.

7147 Basal zone of Domengine formation immediately north of Oil City.

7174 On west line of Sec. 17, north of Oil City, in first canyon south of triangulation Station 2126, in basal horizon of Domengine formation. Coll. B. L. Clark.

7175 Near south line of Sec. 29, T. 18 S., R. 15 E., where Domengine Creek cuts through the formation; basal zone. Coll. B. L. Clark.

7176 On sharp strike ridge of Domengine sandstone where Domengine Creek cuts through Domengine sandstone in Sec. 29, T. 18 S., R. 15 E. Coll. B. L. Clark.

A-973 Base of the Domengine formation on the north bank of Domengine Creek, Sec. 30, T. 19 S., R. 15 E. Coll. F. E. Turner.

A-977 Base of Domengine formation in a draw east of Oil City and 8 miles due north of Coalinga. Coll. F. E. Turner.

A-979 400 yards N. W. of "D" in Domengine Creek, 30 feet above base of the formation. Sec. 30, T. 19 S., R. 15 E. Coll. J. L. Nicholson.

A-1008 Crest of 1800 foot hill near S. E. corner of Sec. 24, T. 18 S., R. 14 E., approximately 12 feet above base of Domengine formation. Coll. H. E. Vokes.

A-1009 Top of 1700 foot hill in center of Sec. 14, T. 18 S., R. 14 E., immediately west of "C" in "Martinez Creek." Coll. H. E. Vokes.

A-1010 Hard brown sandstone outcropping approximately 30 feet below summit of hill on ridge extending N. W. from locality A-1009, near center of N. W. ¼ of Sec. 14, T. 18 S., R. 14 E., opposite small canyon entering valley to the south. Coll. H. E. Vokes.

A-1218 Base of the Domengine formation, on saddle between 2126 foot hill and slightly lower hill to west, on center of line between Secs. 16 and 17, T. 19 S., R. 15 E. Coll. H. E. Vokes.

A-1219 Base of Domengine formation on west side, near top, of long ridge extending N. W. of 2126-foot hill on line between Secs. 9 and 16, T. 19 S., R. 15 E. Coll. H. E. Vokes.

A-1220 First small draw cutting ridge of locality A-1219, at base of Domengine formation. 1/16 inch, on map, north of line between Secs. 9 and 16, Coll. H. E. Vokes.

A-1221 Base of Domengine in small draw at main N. W. tributary entering stream mapped near center of N. E. ¼ of Sec. 9, T. 19 S., R. 15 E. Coll. H. E. Vokes.

* The "quadrangles" cited are those so designated on the topographic maps of the United States Geological Survey.

Localities in eastern end of Vallecitos syncline:

All localities entered from Priest Valley Quadrangle, 1927 edition. Collections by H. E. Vokes.

Basal member:

A-1012 Gray sandstone float boulders in De Los Reyes Canyon, S. E. ¼ of S. E. ¼ of Sec. 16, T. 17 S., R. 12 E.

A-1014 Approximately 300 feet N. W. of highest point on 2600-foot hill, on small flat at head of draw entering De Los Reyes Canyon from the southeast. N. W. corner of N. W. ¼ of S. E. ¼ of Sec. 15, T. 17 S., R. 12 E.

A-1015 300 feet north of locality A-1014, on same stratigraphic horizon.

A-1016 5 feet below top of 2600-foot hill on S. E. side, at edge of S. E. ¼ and N. W. ¼ of Sec. 15, T. 17 S., R. 12 E. Stratigraphically equivalent to localities A-1014 and A-1015.

A-1019 Base of Domengine formation in first draw entering De Los Reyes Canyon from North. At base of a 2200-foot hill at south edge of Sec. 16, T. 17 S., R. 12 E.

A-1023 2500-foot elevation at base of Domengine in first canyon immediately west of 2600-foot hill. Center of E. side of Sec. 15 and W. side of Sec. 14, T. 17 S., R. 12 E.

A-1026 Float-boulder in Tumey Gulch approximately ¼ mile north of Schmaine Ranch House, which is at center of N. edge of Sec. 10, T. 17 S., R. 12 E.

A-1027 On Valdes Ranch, on Silver Creek, center of E. part of S. W. ¼ of Sec. 4, T. 16 S., R. 12 E. Approximately where 120° 40′ parallel crosses most northerly intermittent stream indicated on Sec. 4.

A-1113 In small draw at base of Domengine approximately 50 feet east of fault which displaces formation in N. W. ¼ of Sec. 21, T. 17 S., R. 12 E.

A-1117 Small draw entering west side of creek flowing into east side of Tumey Gulch near N. line of Sec. 10, T. 17 S., R. 12 E. The locality is 100 feet up the draw on N. ¼ of the line between Secs. 10 and 11.

A-1118 At bottom and near head of canyon entering Tumey Gulch between the "m" and "e" of "Tumey," at 2500-foot elevation near W. edge of N. E. ¼ of Sec. 3, T. 17 S., R. 12 E.

A-1120 At extreme south end of ridge of locality A-1016, and approximately 18 feet stratigraphically below it.

A-1122 Approximately on contact between Domengine and Capay horizons on well-marked cattle-trail 75 feet below the crest of the S. end of the hill of locality A-1120.

Upper member:

A-1011 *Ostrea idriaensis* in float in De Los Reyes Canyon, in S. E. ¼ of S. E. ¼ of Sec. 16, and N. W. ¼ of N. E. ¼ of Sec. 21, T. 17 S., R. 12 E.

A-1017 Top of small ridge 800 feet southwest of 2200-foot hill near center of S. edge of Sec. 16, T. 17 S., R. 12 E.

A-1018 Approximately 50 feet below top of Domengine, above uppermost "chocolate-brown" shale zone. A 4-foot bed of large *Ostrea idriaensis;* on line between N. E. and N. W. ¼ of Sec. 15, T. 17 S., R. 12 E., at head of small draw north of the 2500-foot hill nearest the divide between De Los Reyes Canyon and Tumey Gulch. Apparent source of material for locality A-1011.

A-1020 Slightly more than half way up the cliff on the east side of San Carlos Creek, 250 feet south of point where New Idria road crosses San Carlos Creek at S. edge of Sec. 16, T. 17 S., R. 12 E.

A-1022 300 feet above the mouth and 20 feet up north wall of small canyon entering San Carlos Creek immediately south of locality A-1020; center of S. edge of Sec. 16, T. 17 S., R. 12 E.

A-1024 *Ostrea* zone 75 to 100 feet south of tool shed at small coal-working at top of canyon wall above coal-horizon. Immediately south of center of N. E. ¼ of Sec. 15, T. 17 S., R. 12 E.

A-1028 *Corbicula* bed 50 feet above New Idria road at small grave yard near center of Sec. 21, T. 17 S., R. 12 E.

A-1029 Approximately half the distance up the canyon which enters San Carlos Creek where 120° 40′ parallel crosses New Idria road. Center of W. edge of S. W. ¼ of Sec. 21, T. 17 S., R. 12 E.; a 6-inch fossil zone between two "chocolate-brown" shale horizons, 20 feet above a coal zone.

A-1100 Zone of small *Ostrea idriaensis* at top of hill at north edge of De Los Reyes Canyon, at head of small draw marked by two conical erosion remnants of white sandstone at edge of east side of the draw.

A-1103 On hill-slope 25 feet above San Carlos Creek, N. 60° W. of old wooden house (first wooden house S. of locality A-1020, directly south of hill of locality A-1017). Approximately 50 feet above base of Domengine.

A-1106 First spur of hill projecting into Tumey Gulch north of Schmaine Ranch House, near "Tu" of "Tumey," on N. central edge of Sec. 10, T. 17 S., R. 12 E. Approximately 60 feet above floor of canyon. Large *Ostrea idriaensis*.

A-1108 On ridge striking N. 50° W. of locality A-1017, at point N. 70° E. of mouth of canyon of locality A-1022; 2000-foot elevation, immediately above massive white sandstone. Stratigraphically equivalent to locality A-1017.

A-1110 Near 120° 40′ parallel on hill above first road-cut in New Idria road east of bend of road at abandoned saloon (easternmost house mapped on San Carlos Creek near 120° 40′ parallel); near base of exposed section.

A-1116 Ridge on north side of canyon running northwest of old saloon, near 2700-foot elevation.

Localities in western end of Vallecitos syncline, Panoche Quadrangle:

A-1152 200 feet above house in small valley, mapped with road, entering Griswold Canyon from East, in Sec. 24, T. 16 S., R. 10 E. Coll. Berthiaume and Vokes.

A-1153 Near center of W. edge of Sec. 23, T. 16 S., R. 10 E., at 2000-foot elevation; on N. E. face of ridge marked by prominent red sandstone capping on west side of Griswold Canyon. Coll. Berthiaume and Vokes.

A-1154 200 feet higher on ridge and 50 feet stratigraphically above locality A-1153. Coll. Berthiaume and Vokes.

A-1366 Calif. State Survey Coll. "10 miles west of Griswold's on road between San Juan and New Idria, southeast of a sheep well." Coll. Gabb and Whitney.

Localities in Coal Mines section, Coalinga Quadrangle:

7154 Echinoderm-Spiroglyphus layer at San Joaquin Coal Mine.

7155 Fossiliferous lens in sandstone below Echinoderm-Spiroglyphus layer at San Joaquin Coal Mine. Sec. 26, T. 20 S., R. 14 E. Coll. F. E. Turner.

7177 Upper fossiliferous ledge at San Joaquin Coal Mine.

A-972 Equivalent to locality 7155. Coll. F. E. Turner.

A-974 Equivalent to locality 7154. Coll. F. E. Turner.

A-1007 Coarse sandstone reef underlying and overlying shales, outcropping in a small gully about 100 yards from its mouth on the north bank of Los Gatos Creek, N. E. ¼ of Sec. 10, T. 20 S., R. 14 E. Coll. Alex Clark.

A-1167 Top of hill due north of marker for S. W. corner of Sec. 26 and N. W. corner of Sec. 35, T. 20 S., R. 14 E., on line between Secs. 26 and 27, near base of Domengine. Coll. H. E. Vokes.

A-1168 On eastern side of small saddle one third mile due north of Sec. post mentioned in locality A-1167, 150 feet above base of formation. Coll. H. E. Vokes.

A-1169 Soft sandstone lens 20 feet stratigraphically below Echinoderm-Spiroglyphus layer at San Joaquin Coal Mine, on south side of canyon. Coll. H. E. Vokes.

A-1222 Echinoderm-Spiroglyphus layer on highest hill between canyons of California and Joaquin Coal Mines. Coll. H. E. Vokes.

A-1223 Fossils in dump at California Coal Mine, on line between Secs. 15 and 22, T. 20 S., R. 14 E. Coll. H. E. Vokes.

A-1306 In small draw entering Los Gatos Creek from south. Coll. Berthiaume.

Localities in Reef Ridge section:

All localities in Cholame Quadrangle, and all except locality A-1164 in T. 23 S., R. 17 E.

4166 About 500 feet east of ranch-house in Big Tar Canyon on E. line of Sec. 18, near point where road crosses creek. Uppermost zone of Domengine formation.
4167 Same location as locality 4166; third reef from base.
4168 Same location as locality 4166; second reef from base.
4169 Same location as locality 4166; basal zone.
4170 On west side of Big Tar Canyon, where it crosses the Eocene section.
A-816 Base of Eocene in first large canyon south of Big Tar Canyon.
A-817 Top of Domengine in first large canyon south of Big Tar Canyon.
A-818 Lower reef-bed on south side of first divide south of Big Tar Canyon along Eocene-Cretaceous contact.
A-819 Lowest reef bed on side of hill just east of and above first saddle south of Big Tar Canyon.
A-975 Second reef above base of Domengine in draw across ridge to south of Big Tar Canyon.
A-1164 Garza Creek, near 2000 foot elevation just N. E. of center of Sec. 10, T. 23 S., R. 16 E., 200 yards west of Reef Ridge Oil Co. Well No. 1.
A-1165 East side of Big Tar Canyon at end of Eocene ridge in second and third fossiliferous zones.
A-1170 On hill due west of Ranch house, near "a" in "Tar Canyon," Sec. 17.
A-1278 Second ridge northwest of Big Tar Canyon, in second fossiliferous layer above base of formation.
A-1279 Near center of north edge of Sec. 20, on hill slope immediately south of point where the Big Tar—McLure Valley road crosses saddle at head of stream running into McLure Valley. Uppermost fossiliferous layer.
A-1280 Same location as locality A-1279, 45± feet stratigraphically below; 4th fossiliferous horizon above base.
A-1281 20 feet stratigraphically below locality A-1280, 3rd fossiliferous horizon above base of formation.
A-1282 35± feet stratigraphically below locality A-1281; second fossiliferous layer above base of formation.
A-1283 18 feet stratigraphically below locality A-1282; lower fossiliferous zone.

Localities in Arroyo Hondo formation north of Coalinga, Coalinga Quadrangle:

1817 S. W. ¼ of N. W. ¼ of Sec. 15, T. 18 S., R. 14 E., 100 feet up the fourth small draw from west end of ridge; immediately opposite the place where Urruttia Canyon enters Salt Creek.
A-820 Less than 50 feet below the contact with the Domengine formation on cliff a little north of point where Domengine Creek crosses the Eocene outcrop. Coll. B. L. Clark.
A-821 In Domengine Canyon, 30 to 40 feet stratigraphically below locality A-820. Coll. B. L. Clark.
A-978 Ragged Valley shale member, below white sandstone on the north side of Domengine Creek, Sec. 30, T. 19 S., R. 15 E. Coll. F. E. Turner.
4178 On road to Domengine Ranch.

LITERATURE CITED

Adams, Arthur, 1820-1878.

1860. On some new genera and species of Mollusca from Japan. Ann. Mag. Nat. Hist. III. **5**: 299–303. Ap 1860.

Adams, Henry, 1813-1877; & Adams, Arthur, 1820-1878.

1853. The genera of recent Mollusca. **1**: (1-256. *pl. 1–32.* [1853]) 65–96. *pl. 9–12.* Je 1853.

Aldrich, Truman Heminway, 1848-1932.

1886. Preliminary report upon the Tertiary fossils of Alabama and Mississippi. Geol. Surv. Ala. Bull. **1**: 15–60. *pl. 1–6.* 1886.

1895. New or little known Tertiary Mollusca from Alabama and Texas. Bull. Am. Paleont. **1**: 53–82. *pl. 2–6* (= *1–5*). 24 Je 1895.

Anderson, Frank Marion, 1863-

1905. A stratigraphic study in the Mount Diablo Range of California. Proc. Calif. Acad. Sci. III. Geol. **2**: 155–248. *pl. 13–35.* 4 D 1905.

1908. A further stratigraphic study in the Mount Diablo Range of California. Proc. Calif. Acad. Sci. IV. **3**: 1–40. 31 O 1908.

-; & Hanna, G Dallas, 1887–

1925. Fauna and stratigraphic relations of the Tejon Eocene at the type locality in Kern County, California. 1–249. *pl. 1–16.* 18 Mr 1925. (Calif. Acad. Sci. Occas. Pap. no. 11.)

1928. Solen novacularis, a name for an Eocene fossil from California. Nautilus **42**: 65, 66. O 1928.

Anderson, Robert Van Vleck, 1884–

1911. Preliminary report on the geology and oil prospects of the Cantua-Panoche region, California. U. S. Geol. Surv. Bull. **431**: 58–87. 1911.

———; & Pack, Robert Wallace, 1885–

1915. Geology and oil resources of the west border of the San Joaquin valley north of Coalinga, California. U. S. Geol. Surv. Bull. **603**: 1–220. *pl. 1–14.* 1915.

Arnold, Ralph, 1875–

1903. The paleontology and stratigraphy of the marine Pliocene and Pleistocene of San Pedro, California. Mem. Calif. Acad. Sci. **3**: 1–420. *pl. 1–37.* 27 Je 1903.

1907. Geology and oil resources of the Summerland district, Santa Barbara County, California. U. S. Geol. Surv. Bull. **321**: 1–93. *pl. 1–17.* 1907.

1909. Paleontology of the Coalinga district, Fresno and Kings counties, California. U. S. Geol. Surv. Bull. **396**: 1–173. *pl. 1–30.* 1909.

-; & Anderson, Robert Van Vleck, 1884–

1908. Preliminary report on the Coalinga oil district, Fresno and Kings counties, California. U. S. Geol. Surv. Bull 357: 1–142. *pl. 1, 2.* 1908.

1910. Geology and oil resources of the Coalinga district, California. U. S. Geol. Surv. Bull. 398: 1–354. *pl. 1–52.* 1910.

———; & Hannibal, Harold, 1889–

1913. The marine Tertiary stratigraphy of the North Pacific coast of America. Proc. Am. Phil. Soc. 52: 559–605. *pl. 37–48.* N 1913.

1914. Dickerson on California Eocene. Science II. 39: 906–908. 19 Je 1914.

Baker, Horace Burrington, 1889–

1923. Notes on the radula of the Neritidae. Proc. Acad. Nat. Sci. Phila. 75: 117–178. *pl. 9–16.* 15 My 1923.

Bartsch, Paul, 1871–

1917. A monograph of West American melanellid mollusks. Proc. U. S. Nat. Mus. 53: 295–356. *pl. 34–49.* 13 Au 1917.

Becker, George Ferdinand, 1847–1919.

1888. Geology of the quicksilver deposits of the Pacific slope. U. S. Geol. Surv. Monog. 13: 1–486. *pl. 1–7. maps 1–14.* 1888.

1889. Summary of the geology of the quicksilver deposits of the Pacific slope. U. S. Geol. Surv. Ann. Rep. 8: 961–985. *pl. 62, 63.* 1889.

Bellardi, Luigi, 1818–1889.

1878. I molluschi dei terreni terziari del Piemonte e della Liguria. Parte II. Mem. Accad. Sci. Torino II. 29: 1–364. *pl. 1–9.* 1878.

Berthiaume, Sheridan Alba, 1910–

1935. Middle Eocene Foraminifera in western Oregon. Proc. Geol. Soc. Am. 1934: 393. Je 1935. (Abstract.)

Bowdich, Thomas Edward, 1791–1824.

1822. Elements of conchology. Part I. Univalves, 1–83. *pl. 1–19.* 1822.

Casey, Thomas Lincoln, 1857–1925.

1904. Notes on the Pleurotomidae, with description of some new genera and species. Trans. Acad. Sci. St. Louis 14: 123–170. 19 My 1904.

Church, Clifford Carl, 1899–

1931. Foraminifera of the Kreyenhagen Shale. Min. Calif. 27: 202–213. Ap 1931.

Clark, Bruce Lawrence, 1880–

1918. Meganos group, a newly recognized division in the Eocene of California. Bull. Geol. Soc. Am. 29: 281–296. 30 Je 1918.

1921. The stratigraphic and faunal relationships of the Meganos group, Middle Eocene of California. Jour. Geol. 29: 125–165. Mr 1921.

1925. Pelecypoda from the marine Oligocene of western North America. Univ. Calif. Publ. Geol. 15: 69–136. *pl. 8–22.* 5 Ja 1925.

1926. The Domengine horizon, Middle Eocene of California. Univ. Calif. Publ. Geol. **16**: 99–118. 4 N 1926.
1934. A new genus and two new species of Lamellibranchiata from the Middle Eocene of California. Jour. Paleont. **8**: 270–272. *pl. 37*. S 1934. (Abstract.)
1935. Santa Susana and Lower Llajas fauna of Ventura County. Proc. Geol. Soc. Am. **1934**: 394. Je 1935. (Abstract.)

———; & **Palmer, Dorothy Bryant (Kemper), 1897–**
1923. Revision of the Rimella-like gastropods from the West Coast of North America. Univ. Calif. Publ. Geol. **14**: 277–288. *pl. 51*. 31 O 1923.

———; & **Vokes, Harold Ernest, 1908–**
1936. Summary of the marine Eocene sequence of western North America. Bull. Geol. Soc. Am. **47**: 851–878. *pl. 1, 2*. 30 Je 1936.

———; & **Woodford, Alfred Oswald, 1890–**
1927. The geology and paleontology of the type section of the Meganos formation (lower Middle Eocene) of California. Univ. Calif. Publ. Geol. **17**: 63–142. *pl. 14–22*. 31 D 1927.

Conrad, Timothy Abbott, 1803–1867.
1855. Report on the fossil shells collected in California by W. P. Blake. (U. S., 33d Congr., 1st Sess., House Ex. Doc. no. 129.) 5–20. 1855.
1858. Descriptions of the fossil shells. Pacif. R. R. Rep. **5**: 317–329. *pl. 2–9*. "1856" [1858].
1860. Descriptions of new species of Cretaceous and Eocene fossils of Mississippi and Alabama. Jour. Acad. Nat. Sci. Phila. II. **4**: 275–298. *pl. 46, 47*. [13] Mr (separately, F) 1860.
1865. Catalogue of the Eocene and Oligocene Testacea of the United States. Am. Jour. Conch. **1**: 1–35. 25 F 1865.
1866. Check list of the invertebrate fossils of North America. Eocene and Oligocene. Smiths Misc. Coll. **7**(200): 1–41. My 1866.

Cooper, James Graham, 1830–1902.
1894. Catalogue of Californian fossils. (Parts II, III, IV, and V.) Calif. State Mining Bur. Bull. **4**: 1–65. *pl. 1–6*. S 1894.
1896. On some new Cretaceous (and Eocene?) Mollusca of California. Proc. Calif. Acad. Sci. II. **6**: 330–337. *pl. 47, 48*. 18 Au 1896.

Cossmann, Alexandre Edouard Maurice, 1850–1925.
1886. Catalogue des coquilles fossiles de l'éocène des environs de Paris. Ann. Soc. Roy. Malac. Belg. **21**: 17–186. *pl. 1–8*. 1886.
1889. Catalogue illustré des coquilles fossiles de l'éocène des environs de Paris. [Quatrième fascicule.] Ann. Soc. Roy. Malac. Belg. **24**: 3–381. 1889.
1893. Notes complémentaires sur la faune éocénique de l'Alabama. Ann. Géol. Paléont. Gregorio **12**: 1–52. *pl. 1, 2*. Aug. 1893.
1895. Essais de paléoconchologie comparée. **1**: 1–159. *pl. 1–7*. F 1895.
1896. Essais de paléoconchologie comparée. **2**: 1–179. *pl. 1–8*. D 1896.

1899. Essais de paléoconchologie comparée. 3: 1–201. *pl. 1–8.* Ap 1899.
1901. Essais de paléoconchologie comparée. 4: 1–293. *pl. 1–9.* O 1901.
1903. Essais de paléoconchologie comparée. 5: 1–215. *pl. 1–9.* D 1903.
1906. Essais de paléoconchologie comparée. 7: 1–261. *pl. 1–14.* Jl 1906.
1913. Rectifications de nomenclature. Rev. Crit. Paléoz. 17: 61–64. Ja 1913.
1916. Paléoconchologie. Rev. Crit. Paléoz. 20: 98–117. Jl 1916.
1921. Essais de paléoconchologie comparée. 12: 1–348. *pl. A–D, 1–6.* 1921.

———; & Peyrot, A.

1912. Conchologie néogénique de l' Aquitaine. Suite. Act. Soc. Linn. Bord. 66: 121–324. *pl. 1–10.* 1912.

———; & Pissarro, Georges

1904. Iconographie complète des coquilles fossiles de l'éocène des environs de Paris. 1: *pl. 1–16.* D 1904.
1906. Iconographie complète des coquilles fossiles de l'éocène des environs de Paris. 1: *pl. 17–38.* 1906.
1911. Iconographie complète des coquilles fossiles de l'éocène des environs de Paris. 2: *pl. 10–45.* 1911.
1913. Iconographie complète des coquilles fossiles de l'èocène des environs de Paris. 2: *pl. 46–65.* 1913.

Cox, Leslie Reginald, 1897–

1927. Neogene and Quarternary Mollusca from the Zanzibar Protectorate. Rep. Palaeont. Zanz. Prot. 1927: 14–102. *pl. 3–19.* 1927.
1930. The fossil fauna of the Samana range and some neighbouring areas: Part VIII. The Mollusca of the Hangu shales. Paleont. Ind. II. 15: 129–222. *pl. 17–22.* 1930.
1931. A contribution to the molluscan fauna of the Laki and basal Khirthar groups of the Indian Eocene. Trans. Roy. Soc. Edinb. 57: 25–92. *pl. 1–4.* 10 Au 1931.

Crook, T. H.; & Kirby, J. M.

1935. Capay formation. Proc. Geol. Soc. Am. 1934: 334, 335. Je 1935. (Abstract.)

Crosse, Joseph Charles Hyppolyte, 1826–1898.

1886. [Bibliographie.] Catalogue illustré des Coquilles fossiles de l'éocène des environs de Paris, faisant suite aux travaux paléontologiques de G. P. Deshayes, par M. Cossmann.—Premier fascicle. Jour. de Conch. 34: 329–333. 1 O 1886.

Cushman, Joseph Augustine, 1881– ; & Hanna, G Dallas, 1887–

1927. Foraminifera from the Eocene near Coalinga, California. Proc. Calif. Acad. Sci. IV. 16: 205–229. *pl. 13, 14.* 22 Ap 1927.

Dall, William Healey, 1845–1927.

1892. Contributions to the Tertiary fauna of Florida. Part II. Trans. Wagner Inst. Sci. 3: 201–473. *pl. 13–22. map.* D 1892.
1902. Synopsis of the family Veneridae and of the North American recent species. Proc. U. S. Nat. Mus. 26: 335–412. *pl. 12–16.* 29 D 1902.

1909. Contributions to the Tertiary paleontology of the Pacific coast. I. The Miocene of Astoria and Coos Bay, Oregon. U. S. Geol. Surv. Prof. Pap. 59: 1–278. *pl. 1–23.* 1909.

1918a. Notes on Chrysodomus and other mollusks from the North Pacific ocean. Proc. U. S. Nat. Mus. 54: 207–234. 5 Ap 1918.

1918b. Notes on the nomenclature of the mollusks of the family Turritidae. Proc. U. S. Nat. Mus. 54: 313–333. 5 Ap 1918.

1919. Descriptions of new species of mollusks of the family Turritidae from the West Coast of America and adjacent regions. Proc. U. S. Nat. Mus. 56: 1–86. *pl. 1–24.* 8 Au 1919.

Deshayes, Gérard Paul, 1795–1875.

1824. Description des coquilles fossiles des environs de Paris. (1: 1–392. 2: 1–814. Atlas pl. 1–106. 1824–37.) 2: 33–56. *pl. 5–8.* Au 1824.

1861. Description des animaux sans vertèbres découverts dans le bassin de Paris. (Livr. 27/28.) 2: 313–432. 20 N 1861.

1865. Description des animaux sans vertèbres découverts dans le bassin de Paris. (Livr. 47/48.) 3: 289–424. *pl. 94–100.* 10 Je 1865.

Dickerson, Roy Ernest, 1878–

1913. Fauna of the Eocene at Marysville Buttes, California. Univ. Calif. Publ. Geol. 7: 257–298. *pl. 11–14.* 29 Ap 1913.

1914a. Fauna of the Martinez Eocene of California. Univ. Calif. Publ. Geol. 8: 61–180. *pl. 6–18.* 13 My 1914.

1914b. The fauna of the Siphonalia sutterensis zone in the Roseburg quadrangle, Oregon. Proc. Calif. Acad. Sci. IV. 4: 113–128. *pl. 11, 12.* 30 D 1914.

1915. Fauna of the type Tejon: its relation to the Cowlitz phase of the Tejon group of Washington. Proc. Calif. Acad. Sci. IV. 5: 33–98. *pl. 1–11.* 15 Je 1915.

1916. Stratigraphy and fauna of the Tejon Eocene of California. Univ. Calif. Publ. Geol. 9: 363–524. *pl. 36–46.* 2 My 1916.

1917. Climate and its influence upon the Oligocene faunas of the Pacific coast, with descriptions of some new species from the Molopophorus lincolnensis zone. Proc. Calif. Acad. Sci. IV. 7: 157–192. *pl. 27–31.* 31 Jl 1917.

Dumble, Edwin Theodore, 1852–1927.

1912. Notes on Tertiary deposits near Coalinga oil field (California) and their stratigraphic relations with the Upper Cretaceous. Jour. Geol. 20: 28–37. 1912.

Durham, John Wyatt

1937. Gastropods of the family Epitoniidae from Mesozoic and Cenozoic rocks of the west coast of North America, including one new species by F. E. Turner and one by R. A. Bramkamp. Jour. Paleont. 11: 479–512. *pl. 56, 57.* 14 S 1937.

Edwards, Frederic Erasmus, 1799–1875.

1866. Pyrula angulata. In Lowry's Chart of the characteristic British Tertiary fossils. *pl. 4.* 1866.

Eldridge, George Homans, 1854–1905.

1903. The petroleum fields of California. U. S. Geol. Surv. Bull. **213**: 306–321. 1903.

Etherington, Thomas John, 1899–

1931. Stratigraphy and fauna of the Astoria Miocene of southwest Washington. Univ. Calif. Publ. Geol. **20**: 31–142. *pl. 1–14. map.* 20 My 1931.

Gabb, William More, 1839–1878.

1861. Synopsis of the Mollusca of the Cretaceous formation, including the geographical and stratigraphical range and synonymy. Proc. Am. Phil. Soc. **8**: 57–257. 1861.

1864. Description of the Cretaceous fossils. Paleontology [of California]. **1**: 55–236. *pl. 9–32.* 1864. (Geol. Surv. Calif.)

1868. An attempt at a revision of the two families Strombidae and Aporrhaidae. Am. Jour. Conch. **4**: 137–149. *pl. 13, 14.* 3 N 1868.

1869. Cretaceous and Tertiary fossils. Paleontology [of California]. **2**: 1–299. *pl. 1–36.* 1869. (Geol. Surv. Calif.)

Gardner, Julia Anna, 1882–

1926a. The molluscan fauna of the Alum Bluff group of Florida. U. S. Geol. Surv. Prof. Pap. **142**: 1–79. *pl. 1–15.* 1926.

1926b. The nomenclature of the superspecific groups of Corbula in the lower Miocene of Florida. Nautilus **40**: 41–47. O 1926.

1935. The Midway group of Texas. 1–403. *pl. 1–28.* "1 Ja 1933" [My 1935]. (Texas Univ. Bull. no. 3301.)

–; & Bowles, Edgar.

1934. Early Tertiary species of gastropods from the Isthmus of Tehuantepec. Jour. Wash. Acad. Sci. **24**: 241–248. 15 Je 1934.

Gester, George Clark, 1884– ; & Galloway, John.

1933. Geology of the Kettleman Hills oil field, California. Bull. Am. Assoc. Petrol. Geol. **17**: 1161–1193. O 1933.

Grabau, Amadeus William, 1870–

1904. Phylogeny of Fusus and its allies. 1–157. *pl. 1–18.* 1904. (Smiths. Misc. Coll. **44**: art. 4.)

Grant, Ulysses Simpson, 1893– ; & Gale, Hoyt Rodney, 1904–

1931. Catalogue of the marine Pliocene and Pleistocene Mollusca of California and adjacent regions. Mem. San Diego Soc. Nat. Hist. **1**: 1–1036. *pl. 1–32.* 3 N 1931.

Gray, John Edward, 1800–1875.

1847a. Description of some new species of marine shells. Jukes' Narrative of the surveying voyage of H. M. S. Fly. **2**: 355–362. *pl. 1, 2.* 1847.

1847b. A list of the genera of recent Mollusca, their synonyma and types. Proc. Zool. Soc. London **1847**: 129–206. N 1847.

Hanna, G Dallas, 1887–

1924. Rectifications of nomenclature. Proc. Calif. Acad. Sci. IV. **13**: 151–186. 18 Mr 1924.

1925. The age and correlation of the Kreyenhagen shale in California. Bull. Am. Assoc. Petrol. Geol. **9**: 990–999. S 1925.

Hanna, Marcus Albert, 1898–

1927. An Eocene invertebrate fauna from the La Jolla quadrangle, California. Univ. Calif. Publ. Geol. **16**: 247–398. *pl. 24–57.* 25 Mr 1927.

Harris, George Frederick, 1862– ; & Burrows, Henry William, 1858–

1891. The Eocene and Oligocene beds of the Paris basin. i-viii. 1–129. *map.* 23 S 1891.

Harris, Gilbert Dennison, 1864–

1893. Correlation of Tejon deposits with Eocene stages of the Gulf slope. Science **22**: 97. 18 Au 1893.

1896. The Midway stage. Bull. Am. Paleont. **1**: 115–270. *pl. 11–25.* 11 Je 1896.

1899. The Lignitic stage. Part II. Scaphopoda, Gastropoda, Pteropoda, and Cephalopoda. Bull. Am. Paleont. **3**: 1–128. *pl. 1–12.* 4 My 1899.

Hedley, Charles, 1862–1926.

1918. A check-list of the marine fauna of New South Wales. Part I. Jour. Roy. Soc. N. S. Wales **51**: M1–M120. 1918.

1922. A revision of the Australian Turridae. Rec. Austral. Mus. **13**: 213–359. *pl. 42–56.* 30 S 1922.

Heilprin, Angelo, 1853–1907.

1887. Explorations on the west coast of Florida and in the Okeechobee wilderness. Trans. Wagner Inst. Sci. **1**: 1–134. *pl. 1–19.* My 1887.

Herrmannsen, August Nicolaus, 1807–1854.

1847. Indicis generum Malacozoorum primordia. **1**: 233–637. 1847.

Hertlein, Leo George, 1898–

1933. A new gryphaeoid oyster from the Eocene of California. Trans. San Diego Soc. Nat. Hist. **7**: 277–280. *pl. 18, f. 5, 6.* 31 Mr 1933.

Iredale, Tom, 1880–

1924. Results from Roy Bell's molluscan collections. Proc. Linn. Soc. N. S. Wales **49**: 179–278. *pl. 33–36.* 24 O 1924.

Jenkins, Olaf Pitt, 1889–

1931. Stratigraphic significance of the Kreyenhagen shale of California. Min. Calif. **27**: 141–186. Ap 1931.

Jousseaume, Félix Pierre, 1835–1921.

1884. Etude sur la famille des Cypraeidae. Bull. Soc. Zool. Fr. **9**: 81–100. 1884.

Jukes-Browne, Alfred Joseph, 1851–

1908. On the genera of Veneridae represented in the Cretaceous and older Tertiary deposits. Proc. Malac. Soc. London 8: 148–177. *f. 1, 2. pl. 6.* 5 N 1908.

King, Philip Parker, 1793–1856.

1831. Description of the Cirrhipedia, Conchifera, and Mollusca, in a collection formed by the officers of H. M. S. Adventure and Beagle employed between the years 1826 and 1830 in surveying the southern coasts of South America, including the Straits of Magalhaens and the coast of Tierra del Fuego. Zool. Jour. 5: 332–349. 1831.

Lamarck, Jean Baptiste Antoine Pierre Monnet de, 1744–1829.

1799. Prodrome d'une nouvelle classification des coquilles. Mém. Soc. Hist. Nat. Paris 69–91. 1799.

1805. Suite des mémoires sur les fossiles des environs de Paris. Ann. Mus. Hist. Nat. Paris 6: 214–221. 1805.

Linnaeus, Carl, 1707–1778.

1758. Systema naturae. Ed. 10. 1: 1–823. 1758.

Merriam, Charles Warren, 1905–

1935. Middle Eocene faunas of northern California. Proc. Geol. Soc. Am. 1934: 392. Je 1935. (Abstract.)

———; & Turner, Francis Earl, 1905–

1937. The Capay Middle Eocene of northern California. Univ. Calif. Publ. Geol. 24: 91–113. *pl. 5, 6* (= 111,113). 4 F 1937.

Montfort, Pierre Denys de, 1768–1820.

1810. Conchyliologie systématique. 2: 1–676. 1810.

Müller, Philipp Ludwig Statius, 1725–1776.

1766. Einleitung zur Erkäntnis der Schnecken und Muscheln. Delic. Nat. Sel. 1: 33–60, 129. *pl. B, B1–B6.* 1766.

Nelson, Richard Newman, 1897–

1925. A contribution to the paleontology of the Martinez Eocene of California. Univ. Calif. Publ. Geol. 15: 397–466. *pl. 49–61.* 24 S 1925.

Olsson, Axel Adolf, 1889–

1922. The Miocene of northern Costa Rica. Bull. Am. Paleont. 9: 173–339. 21 Ap; 341–481. *pl. 4–35.* 21 Je 1922.

Orbigny, Alcide Dessalines d', 1802–1857.

1844. Paléontologie francaise. Terrains crétaces. 3: (1–807. *pl.* 237–489. "1843" [1844–48].) 1–288. 1844.

Packard, Earl Leroy, 1885–

1916. Mesozoic and Cenozoic Mactrinae of the Pacific coast of North America. Univ. Calif. Publ. Geol. 9: 261–360. *pl. 12–35.* 1 My 1916.

1923. An aberrant oyster from the Oregon Eocene. Univ. Oregon Publ. 2(4): 1–14. *pl. 1–4.* 17 D 1923.

Palmer, Dorothy Bryant (Kemper), 1897–

1923. A fauna from the Middle Eocene shales near Vacaville, California. Univ. Calif. Publ. Geol. **14**: 289–318. *pl. 52–57.* 3 N 1923.

Pease, William Harper, 18— –1871.

1860. Descriptions of seventeen new species of marine shells, from the Sandwich Islands, in the collection of Hugh Cuming. Proc. Zool. Soc. London **1860**: 397–400. 1860.

1869. Descriptions of new species of marine Gasteropodae inhabiting Polynesia. Am. Jour. Conch. **5**: 64–79. 7 O 1869.

Pilsbry, Henry Augustus, 1862–

1922. Revision of W. M. Gabb's Tertiary Mollusca of Santo Domingo. Proc. Acad. Nat. Sci. Phila. **73**: 305–435. *pl. 16–47.* Ja 1922.

———; & Sharp, Benjamin, 1858–1915.

1897. Scaphopoda. In Tryon's Manual of conchology. **17**: (1–280. *pl. 1–39.* 1897–98) 1–80. *pl. 1–9.* 11 My 1897; 81–144. *pl. 10–26.* 15 O 1897.

Reed, Ralph Daniel

1924. Role of heavy minerals in the Coalinga Tertiary formations. Econ. Geol. **19**: 730–749. 15 D 1924.

Reinhart, Philip Wingate, 1905–

1935. Classification of the pelecypod family Arcidae. Bull. Mus. Hist. Nat. Belg. **11**(13): 1–68. *pl. 1–5* (= 59–63). Au 1935.

1937. Cretaceous and Tertiary pelecypods of the Pacific slope incorrectly assigned to the family Arcidae. Jour. Paleont. **11**: 169–180. *pl. 27.* Ap 1937. (Abstract.)

Risso, Joseph Antoine, 1777–1845.

1826. Histoire naturelle des principales productions de l'Europe méridionale. **4**: i–vii. 1–439. *pl. 1–12.* 1826.

Roeding, Peter Friedrich, 1767–1846.

1798. Museum Boltenianum. Pars secunda continens Conchylia. i–viii. 1–199. 1798.

Say, Thomas, 1787–1834.

1822. An account of some of the marine shells of the United States. Jour. Acad. Nat. Sci. Phila. **2**: 221–248. Je 1822.

Schenck, Hubert Gregory, 1897–

1926. Cassidae of western America. Univ. Calif. Publ. Geol. **16**: 69–98. *pl. 12–15.* 4 My 1926.

1931. Cephalopods of the genus Aturia from western North America. Univ. Calif. Publ. Geol. **19**: 435–490. *pl. 66–78.* 21 Ja 1931.

1936. Nuculid bivalves of the genus Acila. 1–149. *pl. 1–18.* Jl 1936. (Geol. Soc. Am. Spec. Pap. no. 4.)

Schilder, Franz Alfred, 1896–

1926a. Additions and corrections to Vredenburg's classification of the Cypraeidae. Rec. Geol. Surv. India **58**: 358–379. "Mr" [Jl] 1926.

1926b. An interesting radula (Eocypraea adamsonii Sow.). Nautilus **40**: 17, 18. Jl 1926.

Schumacher, Heinrich Christian Friedrich, 1758–1830.

1817. Essai d'un nouveau système des habitations des vers testacés. 1–287. *pl. 1–22.* 1817.

Soot-Ryen, Tron, 1896–

1932. Pelecypoda, with a discussion of possible migrations of arctic pelecypods in Tertiary times. Norwegian N. Polar Exped. "Maud" Sci. Res. **5** (12): 1–36. *pl. 1, 2.* 1932. (Also as Medd. Zool. Mus. Oslo no. 23.)

Stanton, Timothy William, 1860–

1893. The Colorado formation and its invertebrate fauna. U. S. Geol. Surv. Bull. **106**: 1–288. *pl. 1–45.* 1893.

1896. The faunal relations of the Eocene and Upper Cretaceous on the Pacific coast. U. S. Geol. Surv. Ann. Rep. **17**(1): 1005–1060. *pl. 63–67.* 1896.

Stearns, Robert Edwards Carter, 1827–1909.

1890. Descriptions of new West American land, fresh water, and marine shells, with notes and comments. Proc. U. S. Nat. Mus. **13**: 205–225. *pl. 15–17.* 16 S 1890.

Stewart, Ralph Bentley, 1901–

1927. Gabb's California fossil type gastropods. Proc. Acad. Nat. Sci. Phila. **78**: 287–447. *pl. 20–32.* 3 Ja 1927.

1930. Gabb's California Cretaceous and Tertiary type lamellibranchs. Spec. Publ. Acad. Nat. Sci. Phila. **3**: 1–314. *pl. 1–17.* 9 Au 1930.

Stoliczka, Ferdinand, 1838–1874.

1868. The Gastropoda [of the Cretaceous rocks of southern India]. Palaeont. Ind. [V.] **2**: (1–498. *pl. 1–28.* 1867–68) 285–498. *pl. 21–28.* 1 O 1868.

Swainson, William, 1789–1855.

1840. A treatise on malacology. i–viii. 1–419. 1840.

Taff, Joseph Alexander, 1862–

1913. Eocene of the Coalinga-Cantua district, Fresno County, California. Bull. Geol. Soc. Am. **24**: 127, 128. 24 Mr 1913. (Abstract.)

Tryon, George Washington, 1838–1888.

1880. Manual of conchology. **2**: 1–289. *pl. 1–70.* 1880.
1883. Manual of conchology. **5**: 1–276. *pl. 1–63.* 1883.
1884. Manual of conchology. **6**: 1–413. *pl. 1–34.* 1884.
1887. Manual of conchology. **9**: 1–488. *pl. 1–71.* 1887.

Turner, Francis Earl, 1905–

1935. Tentative correlation of the marine Eocene of western Oregon. Proc. Geol. Soc. Am. **1934**: 391, 392. Je 1935. (Abstract.)

1938. Stratigraphy and Mollusca of the Eocene of western Oregon. i–ix. 1–130. *pl. 1–22.* 1 Je 1938. (Geol. Soc. Am. Spec. Pap. no. 10.)

Turner, Henry Ward, 1857–1937; & Stanton, Timothy William, 1860–

1894. Notes on the geology of the coast ranges of California. Am. Geol. **14:** 92–98. Au 1894.

Valenciennes, Achille, 1794–1865.

1833. Coquilles univalves marines de l'Amérique équinoxiale, recueillies pendant le voyage de MM. de Humboldt et Bonpland. In Humboldt & Bonpland's Recueil d'observations de zoologie et d'anatomie comparée. **2:** 262–339. 1833.

Vokes, Harold Ernest, 1908–

1935a. Notes on the variation and synonymy of Ostrea idriaensis Gabb. Univ. Calif. Publ. Geol. **23:** 291–303. *pl. 22–24* (= 299, 301, 303). 15 Mr 1935.

1935b. The genus Velates in the Eocene of California. Univ. Calif. Publ. Geol. **23:** 381–389. *pl. 25, 26* (= 387,389). 15 Mr 1935.

1935c. Stratigraphic position of the Turritella andersoni zone, north of Coalinga. Proc. Geol. Soc. Am. **1934:** 393. Je 1935. (Abstract.)

1937. The gastropod genus Harpa in the Eocene of the western United States. Jour. Paleont. **11:** 10–12. *pl. 2, f. 1–9.* 22 Ja 1937.

Von Estorff, Fritz E.

1930. Kreyenhagen shale at the type locality, Fresno County, California. Bull. Am. Assoc. Petrol. Geol. **14:** 1321–1336. O 1930.

Vredenburg, Ernest Watson, 1870–

1920. Classification of the recent and fossil Cypraeidae. Rec. Geol. Surv. India **51:** 65–152. N 1920.

Waring, Clarence Almon, 18— –1918.

1914. Eocene horizons of California. Jour. Geol. **22:** 781–785. D 1914.

1917. Stratigraphic and faunal relations of the Martinez to the Chico and Tejon of southern California. Proc. Calif. Acad. Sci. IV. **7:** 41–124. *pl. 7–16.* 30 Jl 1917.

Watts, William Lord, 1850–

1894. The gas and petroleum yielding formations of the central valley of California. Bull. Calif. State Mining Bur. **3:** 1–100. Au 1894.

Weaver, Charles Edwin, 1880–

1905. Contribution to the palaeontology of the Martinez group. Univ. Calif. Publ. Geol. **4:** 101–123. *pl. 12, 13.* F 1905.

1912. A preliminary report on the Tertiary paleontology of western Washington. Wash. Geol. Surv. Bull. **15:** 1–80. *pl. 1–15.* 1912.

1916. Tertiary faunal horizons of western Washington. Univ. Wash. Publ. Geol. **1:** 1–67. *pl. 1–5.* F 1916.

———; & Palmer, Katherine Evangeline Hilton (Van Winkle), 1895–

1922. Fauna from the Eocene of Washington. Univ. Wash. Publ. Geol. **1**(3): 1–56. *pl. 8–12.* Je 1922.

White, Charles Abiathar, 1826–1910.

1884. A review of the fossil Ostreidae of North America; and a comparison of the fossil with the living forms. U. S. Geol. Surv. Ann. Rep. **4**: 273–430. *pl. 34–82.* 1884.
1885. On the Mesozoic and Cenozoic paleontology of California. U. S. Geol. Surv. Bull. **15**: 1–33. 5 My 1885.
1889. On invertebrate fossils from the Pacific coast. U. S. Geol. Surv. Bull. **51**: 1–102. *pl. 1–14.* 1889.

Whitfield, Robert Parr, 1828–1910.

1892. Gasteropoda and Cephalophora of the Raritan clays and greensand marls of New Jersey. U. S. Geol. Surv. Monog. **18**: 1–402. *pl. 1–50.* 1892.

Whitney, Josiah Dwight, 1819–1896.

1865. Geology [of California]. **1**: 1–498. *pl. 1–9.* 1865. (Geol. Surv. Calif.)
1869. Preface. Paleontology [of California]. **2**: vii–xiv. 1869. (Geol. Surv. Calif.)

Woodring, Wendell Phillips, 1891–

1925. Miocene mollusks from Bowden, Jamaica. Pelecypods and scaphopods. 1–222. *pl. 1–28.* 20 My 1925. (Carnegie Inst. Wash. Publ. no. 366.)
1928. Miocene mollusks from Bowden, Jamaica. Part II. Gastropods and discussion of results. 1–564. *pl. 1–40.* 28 N 1928. (Carnegie Inst. Wash. Publ. no. 385.)

Wrigley, Arthur

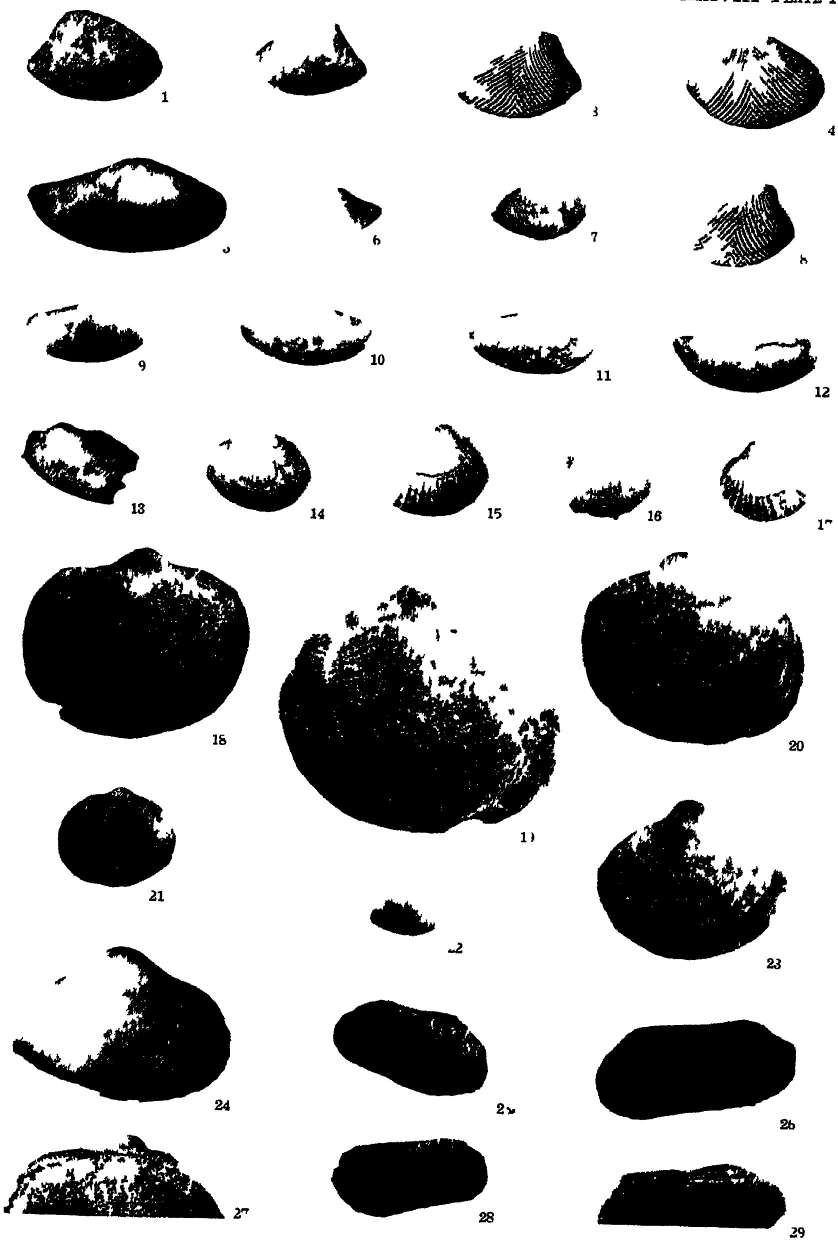
1929. Notes on English Eocene Mollusca. III. Ficus. Proc. Malac. Soc. London **18**: 235–251. *pl. 15, 16.* 15 Jl 1929.
1934. English Eocene and Oligocene Cassididae, with notes on the nomenclature and morphology of the family. Proc. Malac. Soc. London **21**: 108–130. *pl. 15–17.* Jl 1934.

EXPLANATION OF PLATES

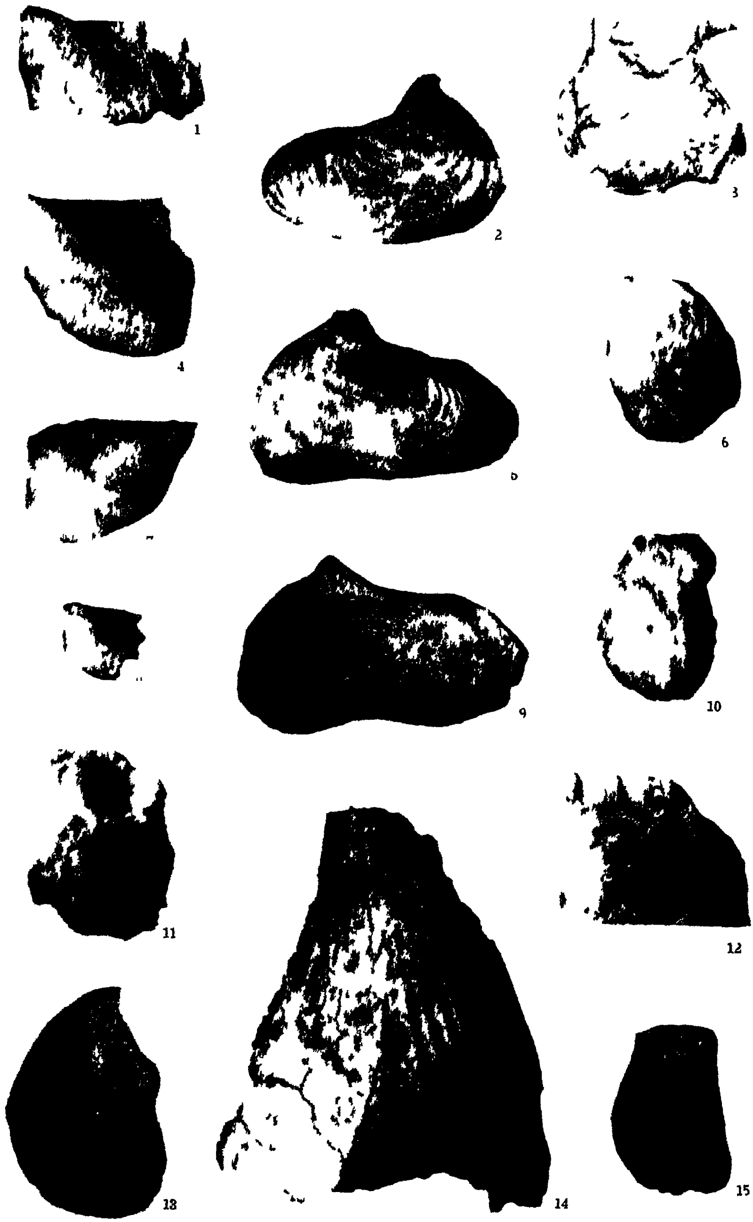
All figured specimens deposited in the University of California Museum of Paleontology, Invertebrate Collections Magnifications approximate.

PLATE 1

FIGURE 1 *Nucula cooperi* Dickerson. × 2, Hypotype 15559, loc 1817
FIGURE 2 *Nucula cooperi* Dickerson × 2, Hypotype 15560, loc 1817
FIGURE 3 *Acila (Truncacila) decisa* (Conrad) × 2 5, Hypotype 15558, loc 1817
FIGURE 4 *Acila (Truncacila) decisa* (Conrad) × 2 5, Hypotype 15557, loc 1817
FIGURE 5 *Calorhadia (Litorhadia) fresnoensis* (Dickerson) × 1 5, Topotype 15563, loc 1817
FIGURE 6 *Jupiteria (Ledina) duttonae* n sp × 2 3, Holotype 15564, loc 1817
FIGURE 7 *Acila (Truncacila) decisa* (Conrad) var × 2, figured specimen 15747, loc A-1165
FIGURE 8 *Acila (Truncacila) decisa* (Conrad) var × 2, figured specimen 15747, loc A-1165
FIGURE 9 *Nuculana (Saccella) hondana* n sp × 2, Holotype 15561, loc 1817
FIGURE 10 *Nuculana (Saccella) hondana* n sp × 2, Paratype 15562, loc 1817
FIGURE 11 *Nuculana (Saccella) chaneyi* n sp × 3 5, Syntype 15745, loc A-1165
FIGURE 12 *Nuculana (Saccella) chaneyi* n sp × 3 5, Syntype 15746, loc A-976
FIGURE 13 *Porterius woodfordi* (M A Hanna) × 1 5, Hypotype 32472, loc 1817
FIGURE 14 *Glycymeris perrini instabilis* (Anderson & Hanna) × 1 9, Hypotype 15570, loc 1817
FIGURE 15 *Glycymeris* cf *rosecanyonensis* M A Hanna × 3 3, Hypotype 32579, loc 672
FIGURE 16 *Glycymeris perrini instabilis* (Anderson & Hanna) × 1 9, Hypotype 15569, loc 1817
FIGURE 17 *Glycymeris fresnoensis* Dickerson × 1, Topotype 15593, loc 1817
FIGURE 18 *Glycymeris sagittata* (Gabb) × 1, Hypotype 15564, loc A-819
FIGURE 19 *Glycymeris sagittata* (Gabb) × 1, Hypotype 15567, loc A-1219
FIGURE 20 *Glycymeris sagittata* (Gabb) × 1, Hypotype 15565, loc 2293
FIGURE 21 *Glycymeris reefensis* n sp × 1 5, Holotype 15571, loc A-1165
FIGURE 22 *Trigonodesma hornii elusa* (Clark & Woodford) × 2 5, Hypotype 15594, loc 1817
FIGURE 23 *Glycymeris perrini* Dickerson × 1 5, Hypotype 31439, loc A-1165
FIGURE 24 *Trigonodesma hornii* (Gabb) × 3, Hypotype 32544, loc 672
FIGURE 25 *Barbatia (Obliquarca) morsei* Gabb × 1 5, Hypotype 32537, loc 7155
FIGURE 26 *Barbatia (Obliquarca) morsei* Gabb × 1 5, Hypotype 15575, loc A-972
FIGURE 27 *Trigonodesma hornii* (Gabb) × 3, (hinge), Hypotype 32544, loc 672
FIGURE 28 *Barbatia (Obliquarca) morsei* Gabb. × 1 5, Hypotype 15573, loc 7155
FIGURE 29 *Barbatia (Obliquarca) morsei* Gabb × 1 5, Hypotype 15574, loc 7155



VOKES EOCENE MOLLUSCA OF CALIFORNIA



VOKES EOCENE MOLLUSCA OF CALIFORNIA

PLATE 2

FIGURE 1. *Pteria pellucida* (Gabb). × 1; Lectotype 11983, Calif. State Survey Coll. no. 198.

FIGURE 2. *Exputens alexi* Clark. × 2; Paratype 32385, loc. A-1007

FIGURE 3. *Pedalion joaquinensis* n. sp. × 1.5; Holotype 15577, loc 7177.

FIGURE 4. *Pteria pellucida* (Gabb). × 1; Hypotype 32623, loc A-975.

FIGURE 5. *Exputens alexi* Clark. × 2; Holotype 32386, loc A-1007.

FIGURE 6. *Pedalion joaquinensis* n. sp × 1; Paratype 15579, loc. 7155.

FIGURE 7. *Pteria pellucida* (Gabb). × 1; Hypotype 32605, loc. A-975

FIGURE 8. *Pteria pellucida* (Gabb). × 1; Lecto-paratype 15576, Calif. State Survey Coll. no. 198.

FIGURE 9. *Exputens alexi* Clark. × 2; Paratype 32384, loc. A-1007.

FIGURE 10. *Pedalion joaquinensis* n. sp. × 1; Paratype 15578, loc. A-972

FIGURE 11. *Ostrea idriaensis* var. *fettkei* Weaver. × 1; Hypotype 15583, loc. A-1022.

FIGURE 12. *Pedalion joaquinensis* n. sp. × 2; Paratype 15581, loc 7177.

FIGURE 13 *Ostrea idriaensis* var *fettkei* Weaver. × 1.5; Hypotype 15582, loc. A-1021.

FIGURE 14. *Pinna* n. sp. × 1; figured specimen 32595, loc. 2287.

FIGURE 15. *Pedalion joaquinensis* n. sp. × 1; Paratype 15580, loc. A-972

PLATE 3

FIGURE 1 *Pecten* (?) n. sp. × 3; figured specimen 15601, loc. A-1012.
FIGURE 2. *Propeamussium mideocenicum* n. sp × 1.5; Syntype 15586, loc. 1817.
FIGURE 3. *Propeamussium mideocenicum* n sp × 1.5; Syntype 15584, loc. 1817
FIGURE 4. *Propeamussium mideocenicum* n. sp. × 1.5; Syntype 15585, loc. 1817
FIGURE 5. *Ostrea* sp. × 1; figured specimen 15744, loc. A-1308
FIGURE 6. *Pododesmus* (*Monia*) *inornatus* (Gabb) × 1; Hypotype 15587, loc. A-1312.
FIGURE 7. *Pododesmus* (*Monia*) *inornatus* (Gabb). × 1.5; Hypotype 15588, loc. A-1312.
FIGURE 8. *Vulsella* (?) *clarki* n. sp. × 2.3; Holotype 15743, loc. 1817.
FIGURE 9. *Pododesmus* (*Monia*) *inornatus* (Gabb). × 1.5; Hypotype 15590, loc A-1101
FIGURE 10. *Spondylus carlosensis* Anderson. Hinge; Hypotype 32708, loc 2293.
FIGURE 11. *Pododesmus* (*Monia*) *inornatus* (Gabb). × 1.5; Hypotype 15589, loc. A-1101.
FIGURE 12. *Mytilus* (?) sp. × .8; figured specimen 15591, loc. A-1168.
FIGURE 13. *Spondylus carlosensis* Anderson. × 1.5; Hypotype 32708, loc. 2293.
FIGURE 14. *Mytilus dichotomus* Cooper. × 1.5; Hypotype 15592, loc. A-1017

VOKES EOCENE MOLLUSCA OF CALIFORNIA

VOKES EOCENE MOLLUSCA OF CALIFORNIA

PLATE 4

FIGURE 1 *Periploma eodiscus* n sp × 1 3; Syntype 15595, loc 4178

FIGURE 2 *Cardiomya dolabraeformis* (Gabb) × 2 5; Holotype 11991, Martinez stage

FIGURE 3 *Periploma eodiscus* n sp × 1 3, Syntype 15596, loc 4178

FIGURE 4 *Crassatella uvasana semidentata* (Cooper) × 1 5; Hypotype 15624, loc 672

FIGURE 5 *Cardiomya domenginica* n sp × 3 5; Holotype 15598, loc A-1027

FIGURE 6 *Crassatella uvasana semidentata* (Cooper) × 1 5, Hypotype 11798, loc 672

FIGURE 7 *Cardiomya silverensis* n sp × 3 5; Holotype 15599, loc A-1027

FIGURE 8 *Crassatella uvasana semidentata* (Cooper) × 1; Hypotype 15602, loc 2291

FIGURE 9 *Cardiomya turneri* n sp × 3 5; Holotype 15597, loc A-1027

FIGURE 10 *Crassatella uvasana semidentata* (Cooper). × 1, Hypotype 15603, loc 2292

FIGURE 11. *Cardiomya* sp. × 3 5, figured specimen 15600, loc 1817

FIGURE 12 *Crassatella uvasana semidentata* (Cooper) × 1; Hypotype 15604, loc A-1219

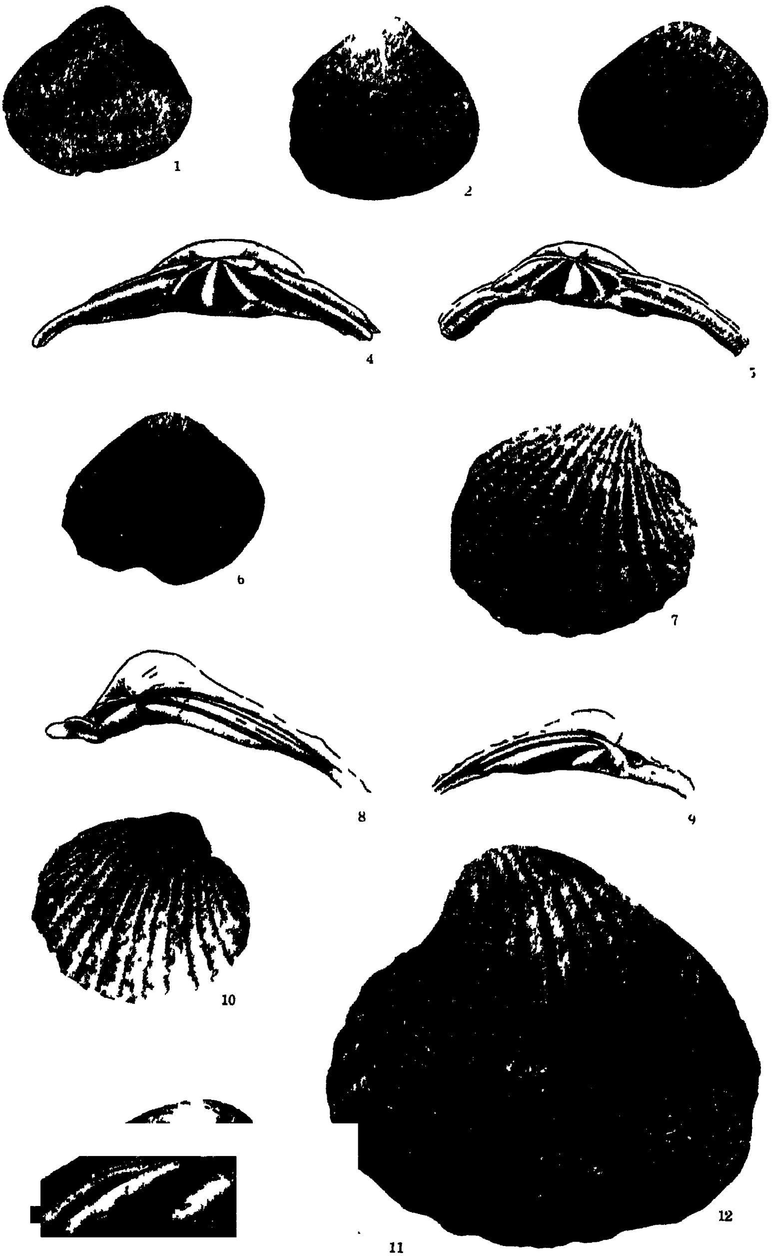
FIGURE 13 *Crassatella* cf *meganosensis* (Clark & Woodford) × 1; Hypotype 30622, loc 2292.

FIGURE 14 *Crassatella mulates* (M A Hanna). × 1; Hypotype 30623, loc 3958.

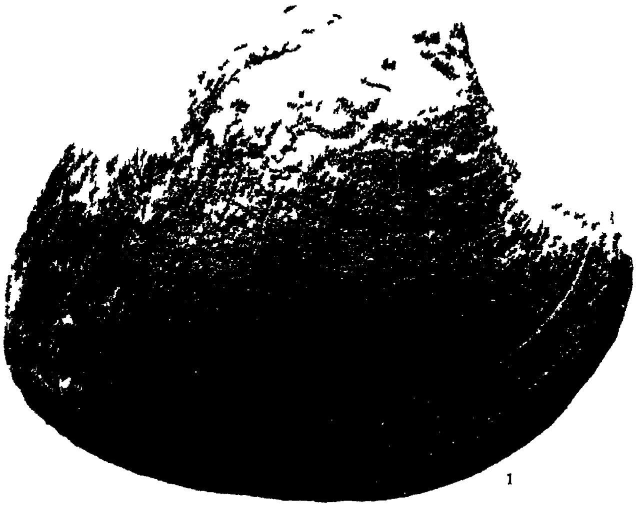
FIGURE 15 *Crassatella mulates* (M A Hanna) × 1; Hypotype 30621, loc. 3958

PLATE 5

FIGURE 1. *Corbicula carlosensis* n. sp. × 1.5; Paratype 15606, loc. A-1028.
FIGURE 2. *Corbicula carlosensis* n. sp. × 1.5; Paratype 15608, loc. A-1028.
FIGURE 3. *Corbicula carlosensis* n. sp. × 1.5; Holotype 15605, loc. A-1028.
FIGURE 4. *Corbicula carlosensis* n. sp. Hinge; Paratype 15609, loc. A-1110.
FIGURE 5. *Corbicula carlosensis* n. sp. Hinge; Paratype 15610, loc. A-1110.
FIGURE 6. *Corbicula carlosensis* n. sp. × 1.5; Paratype 15607, loc. A-1028.
FIGURE 7. *Venericardia* (*Glyptoactis* ?) *domenginica* n. sp. × 1.5; Holotype 15611, loc. A-1219.
FIGURE 8. *Venericardia* (*Glyptoactis* ?) *domenginica* n. sp. Hinge; Paratype 15613, loc. A-1003.
FIGURE 9. *Venericardia* (*Glyptoactis* ?) *domenginica* n. sp. Hinge; Paratype 15612, loc. A-1003.
FIGURE 10. *Megacardita* (*Venericor*) *vallecitosensis* n. sp. × 1; Paratype 15615, loc. A-1022.
FIGURE 11. *Megacardita* (*Venericor*) *vallecitosensis* n. sp. × 1; Holotype 15614, loc. A-1022.
FIGURE 12. *Megacardita* (*Venericor*) *vallecitosensis* n. sp. × 1; Holotype 15614, loc. A-1022.



VOKES: EOCENE MOLLUSCA OF CALIFORNIA



1

2

3

VOKES EOCENE MOLLUSCA OF CALIFORNIA

PLATE 6

FIGURE 1 *Megacardita (Venericor) aragonia smileyi* n subsp × 1, Holotype 15626, loc 672

FIGURE 2 *Megacardita (Venericor) aragonia smileyi* n subsp Hinge, Holotype 15626, loc 672

FIGURE 3 *Megacardita (Venericor) aragonia smileyi* n subsp Hinge, Paratype 15627, loc 672

PLATE 7

FIGURE 1 *Megacardita (Venericor) hornii carlosensis* n subsp × 1, Holotype 15619, loc A-1017

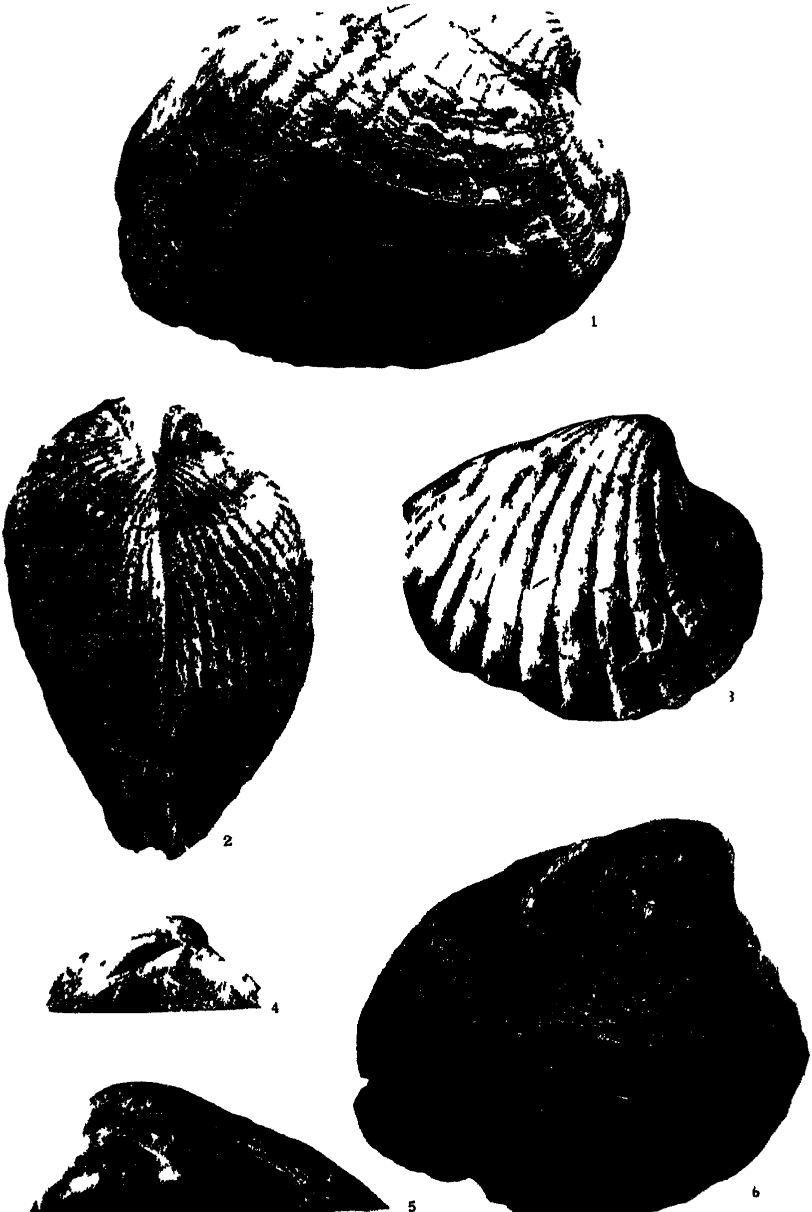
FIGURE 2 *Megcardita (Venericor) hornii carlosensis* n subsp × 1, Holotype 15619, loc A-1017

FIGURE 3 *Megacardita (Venericor) hornii carlosensis* n subsp × 1; Paratype 15621, loc A-1017

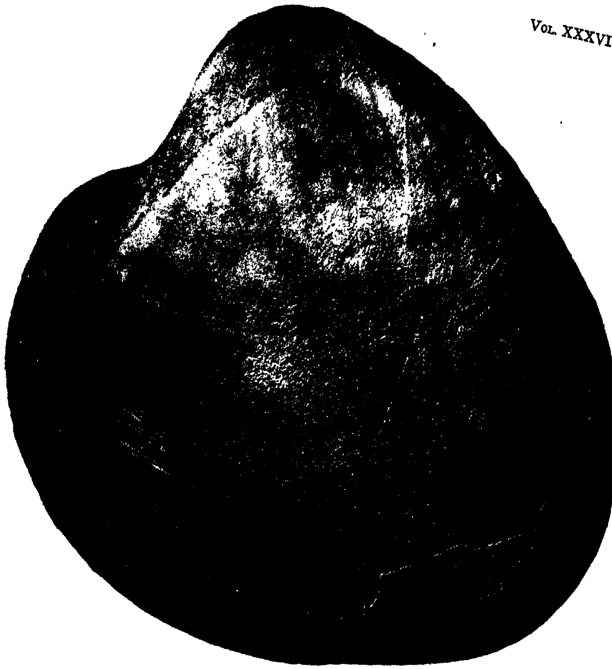
FIGURE 4 *Megacardita (Venericor) hornii carlosensis* n subsp × 1, Paratype 15622, loc A-1017

FIGURE 5 *Megacardita (Venericor) hornii carlosensis* n subsp × 1, Paratype 15620, loc A-1017

FIGURE 6 *Megacardita (Venericor) hornii carlosensis* n subsp × 1; Paratype 15620, loc A-1017



VOKES: EOCENE MOLLUSCA OF CALIFORNIA



1

VOKES: EOCENE MOLLUSCA OF CALIFORNIA

PLATE 8

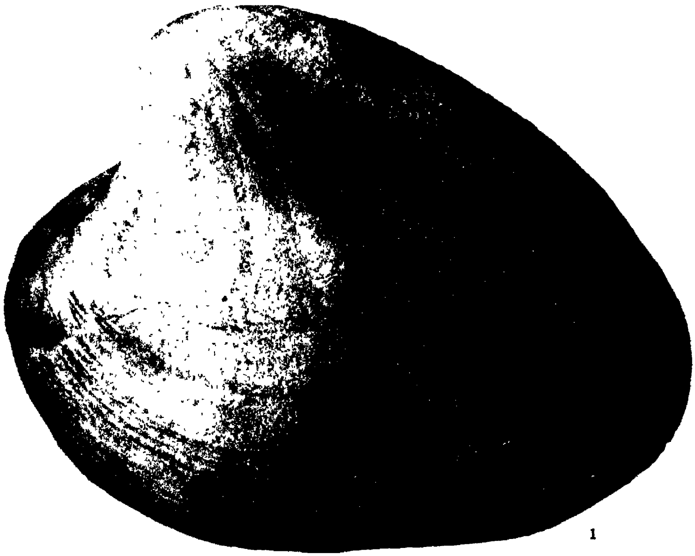
FIGURE 1. *Megacardita* (*Venericor*) *hornii joaquinensis* n. subsp. × 1; Holotype 15616, loc. 4170.

FIGURE 2. *Megacardita* (*Venericor*) *hornii joaquinensis* n. subsp. × 1; Paratype 15618, loc. A-819.

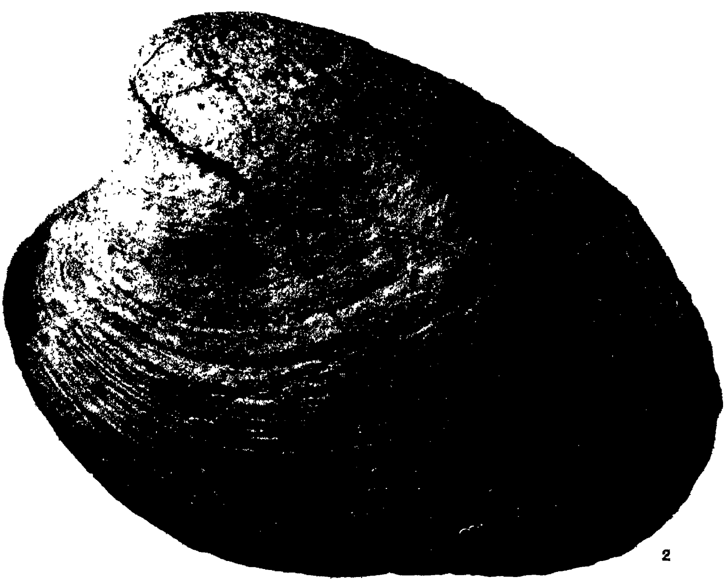
PLATE 9

FIGURE 1. *Megacardita (Venericor) hornii joaquinensis* n. subsp. × 1; Paratype 15617, loc. 4169.

FIGURE 2. *Megacardita (Venericor) hornii joaquinensis* n. subsp. × 1; Paratype 15618, loc. A-819.



1



2

VOKES: EOCENE MOLLUSCA OF CALIFORNIA

VOKES EOCENE MOLLUSCA OF CALIFORNIA

PLATE 10

FIGURE 1 *Lucina (Here) taffana* (Dickerson) × 3 5, Holotype 11789, loc 672.
FIGURE 2 *Lucina (Here) taffana* (Dickerson) × 3 5, Topotype 32828, loc 672
FIGURE 3 *Lucina (Here) taffana* (Dickerson) Hinge, Topotype 32828, loc 672
FIGURE 4 *Taras unisulcata* n sp × 3 7, Holotype 15636, loc 672
FIGURE 5 *Lucina (Here) taffana* (Dickerson) Hinge, Holotype 11789, loc 672
FIGURE 6 *Taras (?) polita* (Gabb) × 3 5, Holotype 11990, Calif State Survey no 243
FIGURE 7 *Taras unisulcata* n sp × 3 7, Paratype 15638, loc 672
FIGURE 8 *Miltha (Eomiltha ?) packi* (Dickerson) × 1, Hypotype 15630, loc A-1015
FIGURE 9 *Lucina (?) bramkampi* n sp × 1 5, Holotype 15629, loc 1817
FIGURE 10 *Taras unisulcata* n sp × 3 7, Paratype 15637, loc 672
FIGURE 11 *Myrtea (Myrtucina) roseburgensis* (Turner) × 1; Hypotype 15632, loc A-1135
FIGURE 12 *Miltha (Eomiltha ?) packi* (Dickerson) × 1, Hypotype 15631, loc A-1016
FIGURE 13 *Myrtea (Myrtucina) roseburgensis* (Turner) × 1; Hypotype 15633, loc A-1135
FIGURE 14 *Myrtea (Myrtucina) roseburgensis* (Turner) Hinge, Hypotype 15635, loc A-1017
FIGURE 15 *Myrtea (Myrtucina) roseburgensis* (Turner) Hinge, Hypotype 15634, loc A-1017

PLATE 11

FIGURE 1. *Plagiocardium* (*Schedocardia*) *brewerii* (Gabb). × 1.5; Hypotype 15642, loc. A-819.

FIGURE 2. *Plagiocardium* (*Schedocardia*) *brewerii* (Gabb). Hinge; Hypotype 15639, loc. 672.

FIGURE 3. *Plagiocardium* (*Schedocardia*) *brewerii* (Gabb). × 1.5; Hypotype 15641, loc. A-1016.

FIGURE 4. *Plagiocardium* (*Schedocardia*) *brewerii* (Gabb). Hinge; Hypotype 15640, loc. A-1010.

FIGURE 5. *Pachydesma packardi* (Dickerson). × 1.5; Topotype 15719, loc. 672.

FIGURE 6. *Nemocardium linteum* (Conrad). Hinge; Hypotype 15645, loc. 672.

FIGURE 7. *Plagiocardium* (*Schedocardia*) *brewerii hartleyense* (Clark & Woodford). × 1.5; Hypotype 15643, loc. 1817.

FIGURE 8. *Pachydesma sulcataria* n. sp. × 1.5; Paratype 15650, loc. A-819.

FIGURE 9. *Nemocardium linteum* (Conrad). × 1.5; Hypotype 15644, loc. 7147.

FIGURE 10. *Pachydesma sulcataria* n. sp. × 1.5; Holotype 15648, loc. A-1022.

FIGURE 11. *Eomeretrix lillisi* (Dickerson). Hinge; Topotype 15653, loc. 1817.

FIGURE 12. *Mercimonia bunkeri* (M. A. Hanna). × 1; Hypotype 32962, loc. 3314.

FIGURE 13. *Pachydesma kelloggensis mclurensis* n.subsp. Hinge; Holotype 15646, loc. A-818.

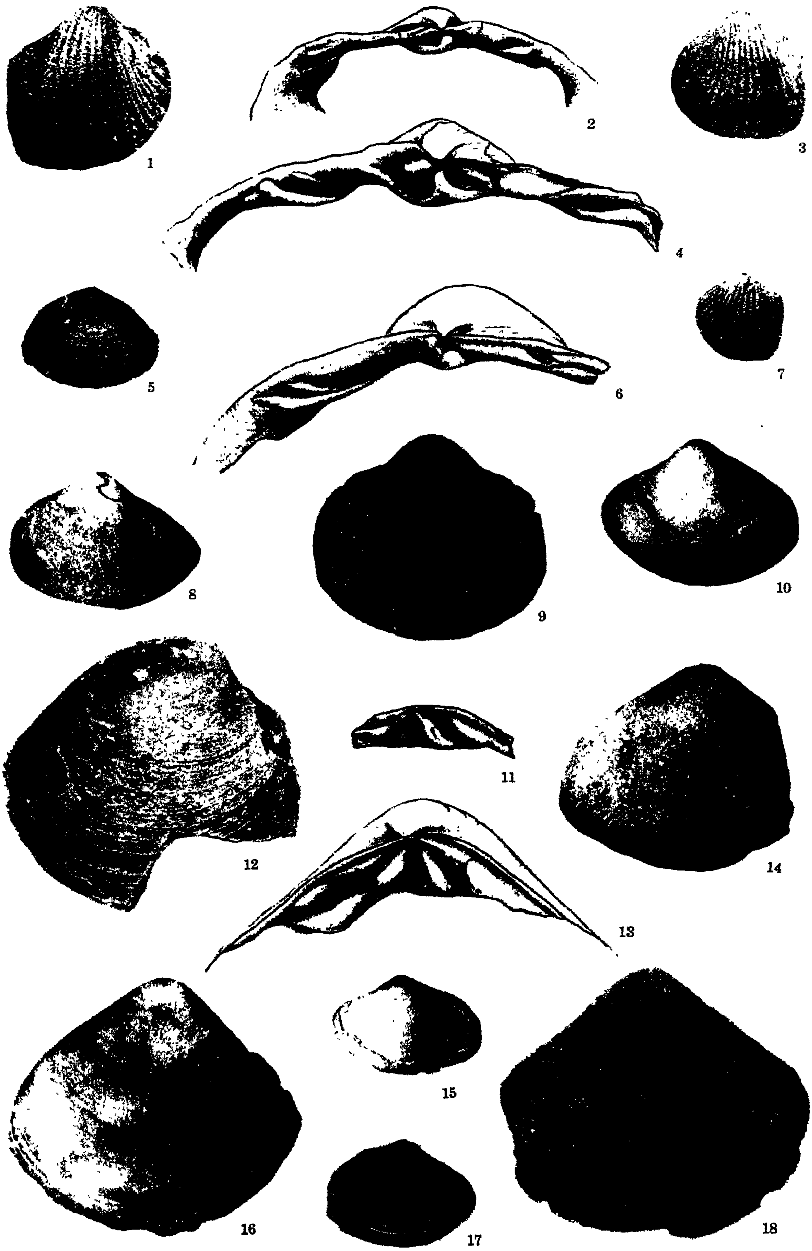
FIGURE 14. *Pachydesma sulcataria* n. sp. × 1.5; Paratype 15649, loc. A-816.

FIGURE 15. *Eomeretrix lillisi* (Dickerson). × 1.5; Topotype 15651, loc. 1817.

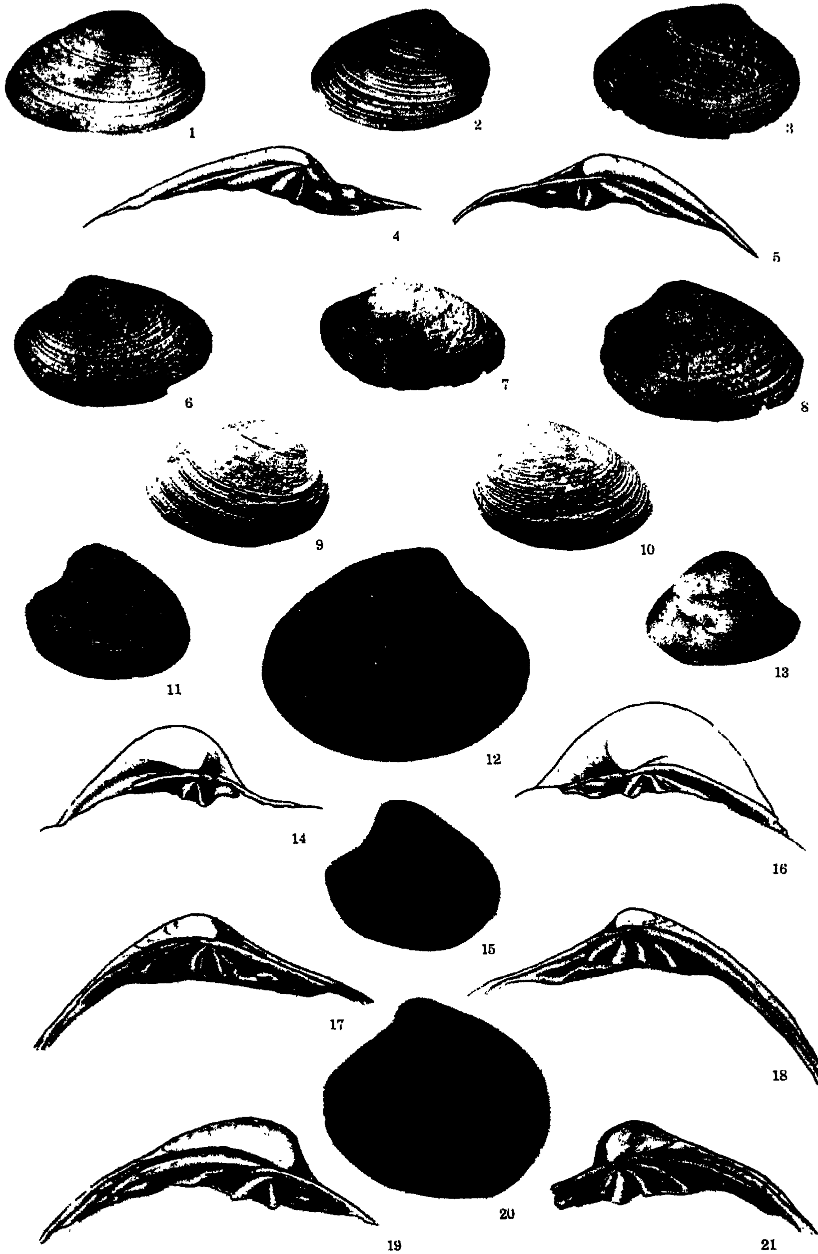
FIGURE 16. *Pachydesma kelloggensis mclurensis* n. subsp. × .9; Paratype 15647, loc. A-1165.

FIGURE 17. *Eomeretrix lillisi* (Dickerson). × 1.5; Topotype 15652, loc. 1817.

FIGURE 18. *Pachydesma kelloggensis mclurensis* n. subsp. × 1; Holotype 15646, loc. A-818.



VOKES: EOCENE MOLLUSCA OF CALIFORNIA



VOKES: EOCENE MOLLUSCA OF CALIFORNIA

PLATE 12

FIGURE 1. *Macrocallista* (*Costacallista*) *domenginica* n. sp. × 1; Holotype 15654, loc. 3315.

FIGURE 2. *Macrocallista* (*Costacallista*) *domenginica* n. sp. × 1; Paratype 15656, loc. A-975.

FIGURE 3. *Macrocallista* (*Costacallista*) *domenginica* n. sp. × 1; Paratype 15655, loc. 3958.

FIGURE 4. *Macrocallista* (*Costacallista*) *domenginica* n. sp. Hinge; Paratype 15657, loc. A-1220.

FIGURE 5. *Macrocallista* (*Costacallista*) *domenginica* n. sp. Hinge; Paratype 15656, loc. A-975.

FIGURE 6. *Macrocallista* (*Costacallista*) *domenginica* n. sp. × 1; Paratype 15658, loc. 3315.

FIGURE 7. *Macrocallista* (*Costacallista*) *domenginica* n. sp. × 1; Paratype 15657, loc. A-1220.

FIGURE 8. *Macrocallista* (*Costacallista*) *domenginica* n. sp. × 1; Paratype 15659, loc. 3315.

FIGURE 9. *Macrocallista* (*Costacallista*) *domenginica capayana* n. subsp. × 1.5; Holotype 15660, loc. 1817.

FIGURE 10. *Macrocallista* (*Costacallista*) *domenginica capayana* n. subsp. × 1.5; Paratype 15661, loc. 1817.

FIGURE 11. *Nitidavenus tejonensis* (Waring). × 1.5; Hypotype 15666, loc. 1817.

FIGURE 12. *Nitidavenus nitida* (Deshayes). × 1.5; Hypotype 15663, Paris Basin, France.

FIGURE 13. *Nitidavenus tejonensis* (Waring). × 1.5; Hypotype 15667, loc. 1817.

FIGURE 14. *Nitidavenus tejonensis* (Waring). Hinge; Hypotype 15669, loc. 1817.

FIGURE 15. *Nitidavenus tejonensis* (Waring). × 1.5; Hypotype 15669, loc. 1817.

FIGURE 16. *Nitidavenus tejonensis* (Waring). Hinge; Hypotype 15668, loc. 1817.

FIGURE 17. *Nitidavenus nitida* (Deshayes). Hinge; Hypotype 15662, Paris Basin, France.

FIGURE 18. *Nitidavenus nitida* (Deshayes). Hinge; Hypotype 15663, Paris Basin, France.

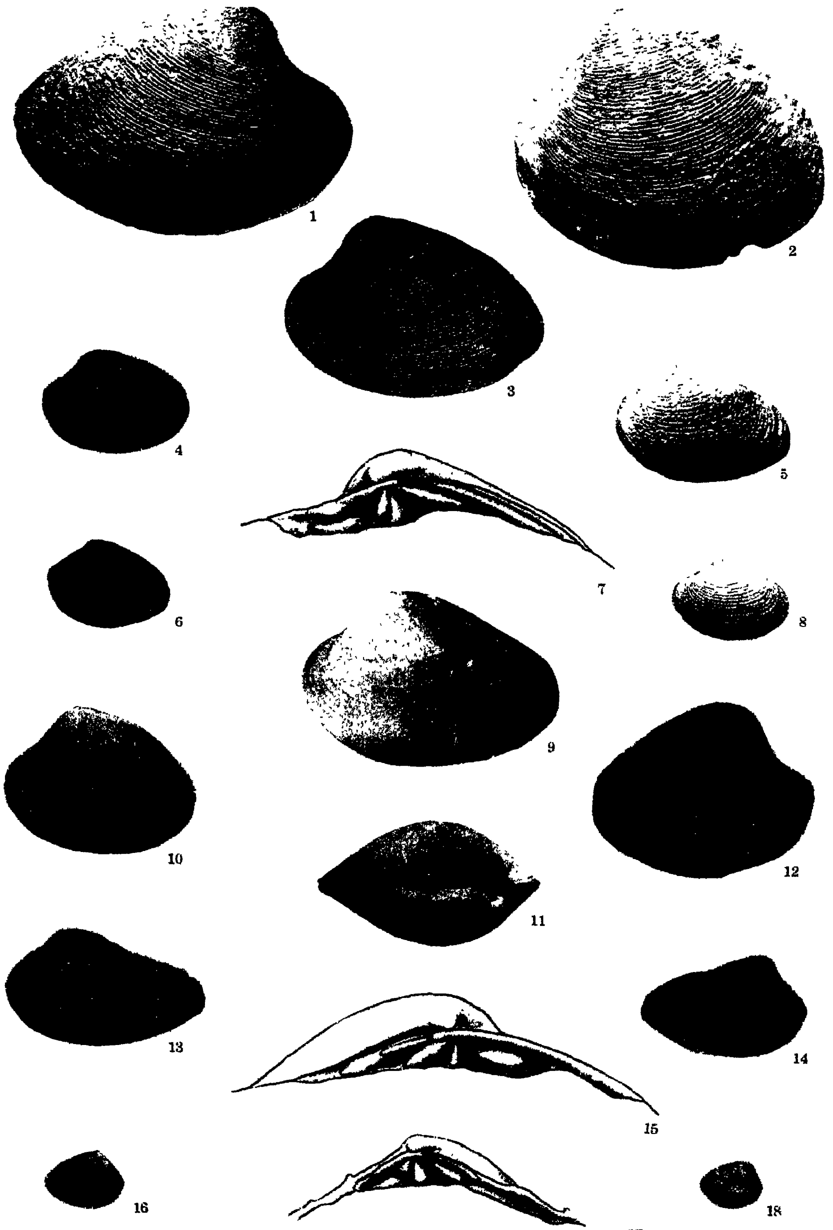
FIGURE 19. *Nitidavenus conradi* (Dickerson). Hinge; Topotype 15664, loc. 1817.

FIGURE 20. *Nitidavenus conradi* (Dickerson). × 1.2; Topotype 15664, loc. 1817.

FIGURE 21. *Nitidavenus conradi* (Dickerson). Hinge; Topotype 15665, loc. 1817.

PLATE 13

FIGURE 1. *Pitar* (*Calpitaria*) *campi* n. sp. × 1; Holotype 15670, loc. 3315.
FIGURE 2. *Pitar* (*Calpitaria*) *campi* n. sp. × 1; Paratype 15671, loc. A-975.
FIGURE 3. *Pitar* (*Calpitaria*) *campi* n. sp. × 1; Paratype 15672, loc. A-975.
FIGURE 4. *Pitar* (*Lamelliconcha*) *avenalensis* n. sp. × 1.5; Paratype 15680, loc. A-975.
FIGURE 5. *Pitar* (*Lamelliconcha*) *avenalensis* n. sp. × 1.5; Holotype 15678, loc. A-1281.
FIGURE 6. *Pitar* (*Lamelliconcha*) *hornii* n. subsp. × 2.2; figured specimen 15878, loc. 672.
FIGURE 7. *Pitar* (*Calpitaria*) *campi* n. sp. Hinge; Paratype 15673, loc. A-1220.
FIGURE 8. *Pitar* (*Lamelliconcha*) *avenalensis* n. sp. × 1.5; Paratype 15679, loc. A-976.
FIGURE 9. *Pitar* (*Lamelliconcha*) *joaquinensis* n. sp. × 1.5; Paratype 15676, loc. A-1027.
FIGURE 10. *Pitar* (*Lamelliconcha*) *joaquinensis* n. sp. × 1.5; Holotype 15674, loc. A-1027.
FIGURE 11. *Pitar* (*Lamelliconcha*) *joaquinensis* n. sp. × 1.5; Paratype 15677, loc. A-1280.
FIGURE 12. *Pitar* (*Lamelliconcha*) *joaquinensis* n. sp. × 1.5; Paratype 15675, loc. 4175.
FIGURE 13. *Tivelina idriaensis* n. sp. × 1.5; Holotype 15681, loc. A-1017.
FIGURE 14. *Tivelina idriaensis* n. sp. × 1.5; Paratype 15682, loc. A-1017.
FIGURE 15. *Tivelina idriaensis* n. sp. Hinge; Holotype 15681, loc. A-1017.
FIGURE 16. *Tivelina* (?) *delicatina* n. sp. × 3; Holotype 15683, loc. A-1108.
FIGURE 17. *Tivelina idriaensis* n. sp. Hinge; Paratype 15682, loc. A-1017.
FIGURE 18. *Tivelina* (?) *delicatina* n. sp. × 3; Paratype 15685, loc. A-1108.



VOKES: EOCENE MOLLUSCA OF CALIFORNIA

VOKES· EOCENE MOLLUSCA OF CALIFORNIA

PLATE 14

FIGURE 1. *Pelecyora gabbi* (Arnold) × 1.5; Topotype 15698, loc. 7155.
FIGURE 2. *Pelecyora gabbi* (Arnold). × 1.5; Topotype 15700, loc. 7155.
FIGURE 3. *Pelecyora gabbi* (Arnold). × 1.5; Topotype 15699, loc. 7155.
FIGURE 4. *Pelecyora aequilateralis* (Gabb). Hinge; Hypotype 15687, loc. A-1020.
FIGURE 5. *Pelecyora gabbi* (Arnold). Hinge; Topotype 15701, loc. 7155.
FIGURE 6. *Pelecyora aequilateralis* (Gabb). × 1.5; Hypotype 15686, loc. A-1020.
FIGURE 7. *Pelecyora aequilateralis* (Gabb). × 1.5; Hypotype 15687, loc. A-1020.
FIGURE 8. *Pelecyora aequilateralis* (Gabb). × 1.5; Hypotype 15688, loc. A-1020.
FIGURE 9. *Pelecyora gabbi* (Arnold). Hinge; Topotype 15702, loc. 7155.
FIGURE 10. *Tellina* sp. × 1.5; figured specimen 15693, loc. 672.
FIGURE 11. *Pelecyora aequilateralis* (Gabb). Hinge; Hypotype 15689, loc. A-1020.
FIGURE 12. *Tellina domenginensis* n. sp. × 1; Paratype 15696, loc. A-975.
FIGURE 13. *Tellina soledadensis* M. A. Hanna. × 1; Hypotype 30664, loc. 672
FIGURE 14. *Tellina domenginensis* n. sp. × 1; Holotype 15694, loc. 3315.
FIGURE 15. *Tellina joaquinensis* Arnold. × 1.5; Topotype 15690, loc. 7155.
FIGURE 16. *Tellina domenginensis* n. sp. × 1; Paratype 15695, loc. A-975.
FIGURE 17. *Gari hornii umpquaensis* Turner × 1; Holotype 33149, loc. A-662.
FIGURE 18. *Tellina domenginensis* n. sp. × 1; Paratype 15697, loc. A-1220.
FIGURE 19. *Tellina joaquinensis* Arnold. × 1.5; Topotype 15692, loc. 7177.
FIGURE 20. *Tellina joaquinensis* Arnold. × 1.5; Topotype 15691, loc. 7155.
FIGURE 21. *Macoma sheridani* n. sp. × 1.5; Holotype 15703, loc. A-1154.
FIGURE 22. *Macoma sheridani* n. sp. × 1.5; Paratype 15704, loc. A-1154.
FIGURE 23. *Gari eoundulata* n. sp. × 1.5; Holotype 15707, loc. A-820.
FIGURE 24. *Gari eoundulata* n. sp. × 1 5; Paratype 15708, loc. A-976.

PLATE 15

FIGURE 1. *Gari texta* Gabb. × 1; Hypotype 33352, loc. 7004.

FIGURE 2. *Gari columbiana* (Weaver & Palmer). × 1 5; Hypotype 15705, loc. A-1027.

FIGURE 3. *Solen* (?) *domengnica* n. sp. × 1; Holotype 15711, loc A-1167.

FIGURE 4. *Solen* (?) *domengnica* n. sp. × 1; Holotype 15711, loc. A-1167. Note dorsal flange.

FIGURE 5. *Solena* (*Eosolen*) *coosensis* Turner × 1 5; Hypotype 15712, loc. A-1280

FIGURE 6. *Solen parallelus* Gabb. × 1; Hypotype 15710, loc. 672.

FIGURE 7. *Solen parallelus* Gabb. × 1.5; Hypotype 15709, loc. A-1009.

FIGURE 8 *Solena* (*Eosolen*) *subverticata* n. sp. × 1.5; Holotype 15713, loc. A-816.

FIGURE 9. *Spisula capayana* n. sp. × 1.5; Syntype 15714, loc. 1817.

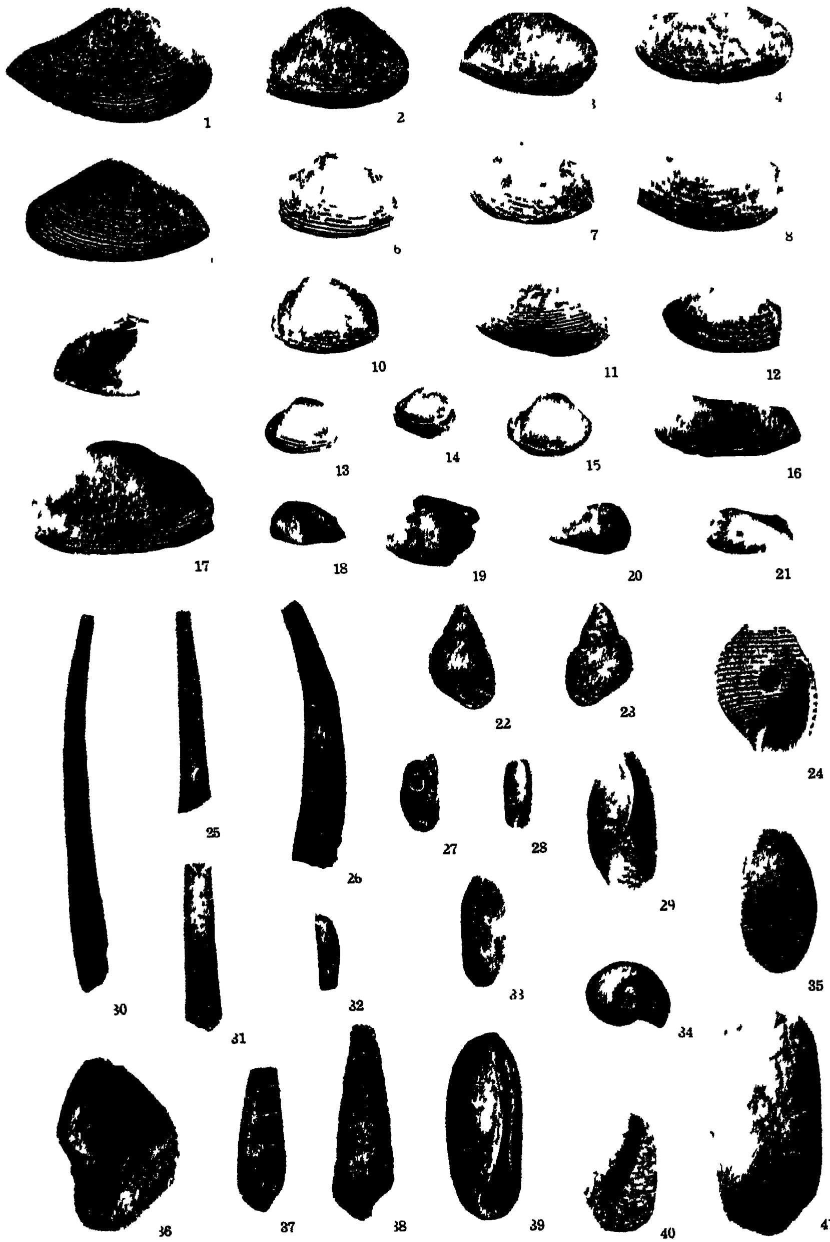
FIGURE 10. *Spisula capayana* n sp. × 1 5; Syntype 15715, loc. 1817.

FIGURE 11. *Spisula capayana* n. sp. × 1 5; Paratype 15716, loc. 1817.

FIGURE 12. *Spisula merriami* Packard. × 1 5; Hypotype 15718, loc. A-1008

FIGURE 13. *Spisula merriami* Packard. × 1.5; Hypotype 15717, loc. A-816.

VOKES EOCENE MOLLUSCA OF CALIFORNIA



VOKES: EOCENE MOLLUSCA OF CALIFORNIA

PLATE 16

FIGURE 1. *Corbula (Caryocorbula) dickersoni* Weaver & Palmer. × 2.2; Hypotype 15721, loc. A-819.

FIGURE 2. *Corbula (Caryocorbula) parilis* Gabb. × 2.2; Hypotype 15723, loc. 1817.

FIGURE 3. *Corbula (Caryocorbula) parilis* Gabb. × 2; Hypotype 15727, loc. A-976.

FIGURE 4. *Corbula domenginica* n. sp. × 3; Syntype 15731, loc. 7155.

FIGURE 5. *Corbula (Caryocorbula) dickersoni* Weaver & Palmer. × 2.2; Hypotype 15720, loc. A-819.

FIGURE 6. *Corbula (Caryocorbula) parilis* Gabb. × 2.2; Hypotype 15724, loc. 1817.

FIGURE 7. *Corbula (Caryocorbula) parilis* Gabb. × 2.2; Hypotype 15726, loc. 1817.

FIGURE 8. *Corbula domenginica* n. sp. × 3.3; Syntype 15730, loc. 7155.

FIGURE 9. *Corbula (Caryocorbula) dickersoni* Weaver & Palmer. × 2.2; Hypotype 15722, loc. 672.

FIGURE 10. *Corbula (Caryocorbula) parilis* Gabb. × 2.2; Hypotype 15725, loc. 1817.

FIGURE 11. *Corbula (Caryocorbula) tomulata* M. A. Hanna. × 2; Hypotype 15728, loc. A-977.

FIGURE 12. *Corbula domenginica* n. sp. × 3.3; Paratype 15732, loc. 7155.

FIGURE 13. *Corbula (Varicorbula) capayana* n. sp. × 3.7; Holotype 15733, loc. 1817.

FIGURE 14. *Corbula (Varicorbula) capayana* n. sp. × 3.7; Paratype 15734, loc. 1817.

FIGURE 15. *Corbula (Varicorbula) capayana* n. sp. × 3.7; Paratype 15735, loc. 1817.

FIGURE 16. *Cuneocorbula torreyensis* (M. A. Hanna). × 3.2; Hypotype 15737, loc. A-1029.

FIGURE 17. *Corbula rosecanyonensis* M. A. Hanna. × 3; Hypotype 15729, loc. 1817.

FIGURE 18. *Cuneocorbula griswoldensis* n. sp. × 3.6; Holotype 15741, loc. A-1154.

FIGURE 19. *Cuneocorbula griswoldensis* n. sp. × 3.6; Paratype 15742, loc. A-1154.

FIGURE 20. *Cuneocorbula torreyensis* (M. A. Hanna). × 3.2; Hypotype 15739, loc. A-1029.

FIGURE 21. *Cuneocorbula torreyensis* (M. A. Hanna). × 3.2; Hypotype 15738, loc. A-1029.

FIGURE 22. *Tornatellaea effingeri* n. sp. × 3.7; Holotype 15754, loc. 1817.

FIGURE 23. *Tornatellaea effingeri* n. sp. × 3.7; Holotype 15754, loc. 1817.

FIGURE 24. *Kleinacteon moodyi* (Dickerson). × 3; Holotype 31177, loc. 672.

FIGURE 25. *Dentalium (Antalis) apicostatum.* n. sp. × 3; Holotype 15747, loc. 672.

FIGURE 26. *Dentalium (Laevidentalium ?) lighti* n. sp. × 3.5; Holotype 15752, loc. 1817.

FIGURE 27. *Cylichna (Cylichnopsis) (?) compara* n. sp. × 2; Holotype 15760, loc. 7155.

FIGURE 28. *Cylichnina tantilla* (Anderson & Hanna). × 2; Hypotype 15759, loc. 672.

FIGURE 29. *Scaphander (Mirascapha) costatus* (Gabb). × 1.5; Hypotype 15756, loc 672

FIGURE 30. *Dentalium (Laevidentalium) calafium* n. sp. × 1.5; Syntype 15750, loc. A-1027.

FIGURE 31. *Dentalium (Laevidentalium) calafium* n. sp. × 3.5; Syntype 15751, loc A-1003

FIGURE 32 *Cadulus* (?) n. sp. × 3.2; figured specimen 15753, loc. 1817.

FIGURE 33. *Cylichnina tantilla* (Anderson & Hanna). × 2; Hypotype 15758, loc. 672.

FIGURE 34. *Akera maga* n. sp. × 2; Holotype 15761, loc. A-1281.

FIGURE 35. *Scaphander (Mirascapha) costatus* (Gabb). × 1 5; Hypotype 15756, loc. 672.

FIGURE 36. *Aturia mylae* (M. A. Hanna). × 2; Hypotype 15877, loc. 1817.

FIGURE 37. *Terebra* n. sp. × 3.7; figured specimen 15767, loc. 1817

FIGURE 38. *Terebra californica* Gabb. × 3.5; Hypotype 15766, loc. 672.

FIGURE 39. *Cylichnina tantilla* (Anderson & Hanna). × 2; Hypotype 15757, loc. 672.

FIGURE 40. *Akera maga* n. sp. × 2; Holotype 15761, loc. A-1281.

FIGURE 41. *Akera maga* n. sp. × 2 3; Paratype 15762, loc. A-976

PLATE 17

FIGURE 1. *Megistostoma gabbianum* (Stoliczka). × 1.7; Hypotype 15763, loc. 672.

FIGURE 2. *Megistostoma gabbianum* (Stoliczka). × 1.7; Hypotype 15765, loc. 1817.

FIGURE 3. *Megistostoma gabbianum* (Stoliczka). × 1.7; Hypotype 15764, loc. A-975.

FIGURE 4. *Fusiturricula (Crenaturricula) crenatospira* (Cooper). × 1; Topotype 12166, loc. 1853.

FIGURE 5. *Fusiturricula (Crenaturricula) crenatospira* (Cooper). × 1; Topotype 12166, loc. 1853

FIGURE 6. *Fusiturricula (Crenaturricula) crenatospira domenginica* n. subsp. × 1 5; Paratype 15769, loc. 3304.

FIGURE 7. *Fusiturricula (Crenaturricula) crenatospira domenginica* n. subsp. × 1; Holotype 15768, loc. 7002.

FIGURE 8. *Surculites mathewsonii* (Gabb). × 1.7; Hypotype 15778, loc. 672.

FIGURE 9. *Eopleurotoma* (?) *traski* n. sp. × 2; Holotype 15770, loc. A-976.

FIGURE 10. *Microsurcula* (?) *ligna* n. sp. × 2.3; Holotype 15773, loc. 7155.

FIGURE 11. *Exilia ucalia* n. sp. × 2; Holotype 15782, loc. A-976.

FIGURE 12. *Eosurcula capayana* n. sp. × 1; Syntype 15900, loc. 1817.

FIGURE 13. *Eosurcula capayana* n. sp. × 2; Syntype 15901, loc. 1817. Cast showing sculpture.

FIGURE 14. *Trypanotoma stocki* (Dickerson). × 2; Topotype 15774, loc. 672.

FIGURE 15. *Pleurofusia fresnoensis* (Arnold). × 2.3; Hypotype 15771, loc. 672.

FIGURE 16. *Pleurofusia fresnoensis* (Arnold). × 2.3; Hypotype 15772, loc. 672.

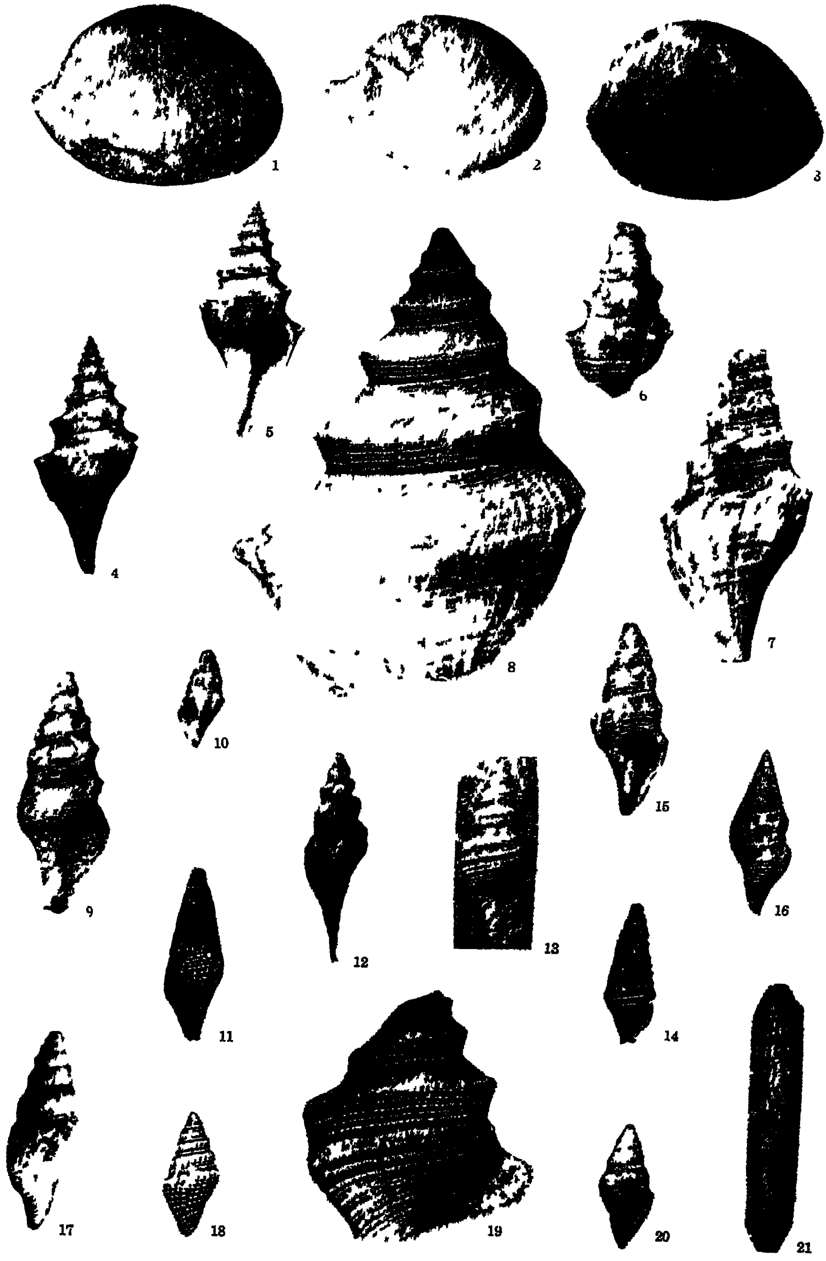
FIGURE 17. *Cryptoconus cooperi* (Dickerson). × 1.5; Hypotype 15780, loc. 4170.

FIGURE 18. *Domenginella claytonensis* (Gabb). × 2; Hypotype 15775, loc. 672.

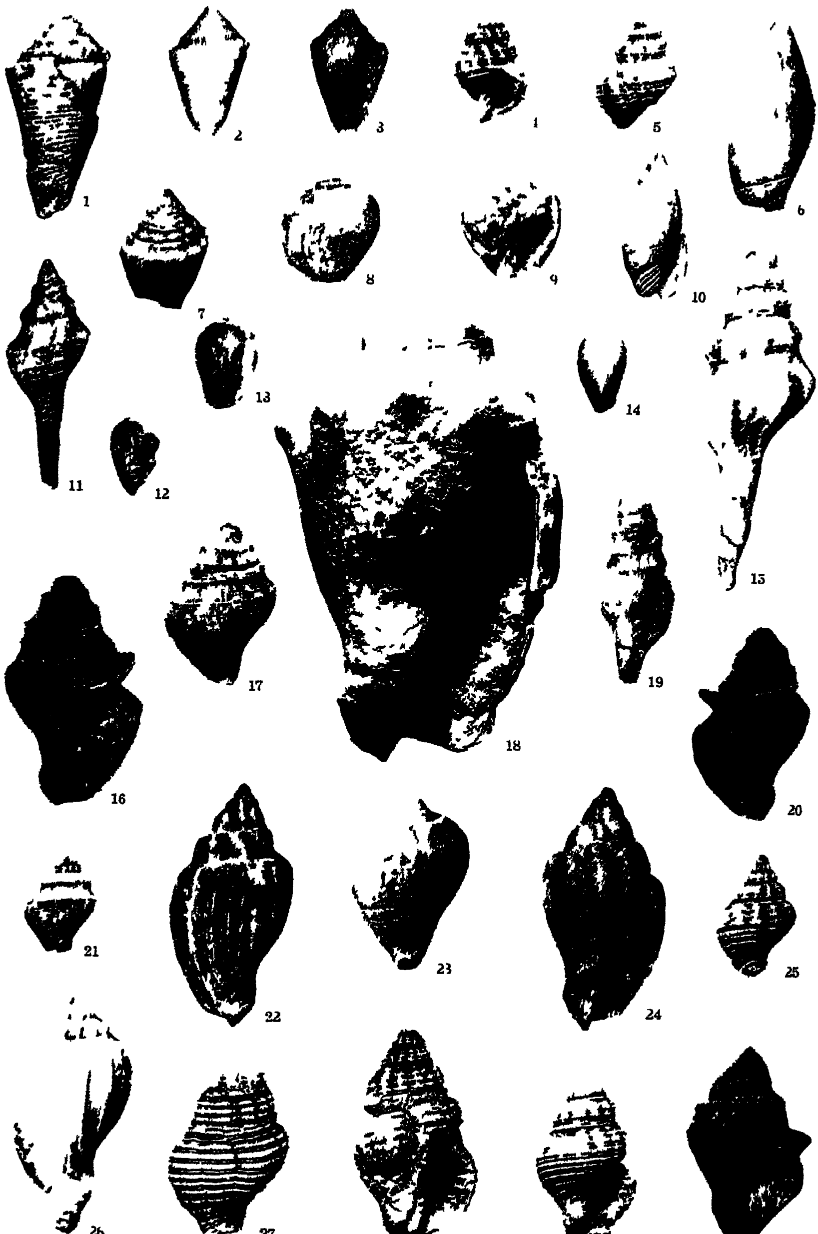
FIGURE 19. *Surculites mathewsonii* (Gabb). × 2; Hypotype 15777, loc. 672.

FIGURE 20. *Domenginella claytonensis* (Gabb). × 2; Hypotype 15776, loc. 672.

FIGURE 21. *Exilia taliaferroi* n. sp. × 2; Holotype 15781, loc. A-978. Cast.



VOKES EOCENE MOLLUSCA OF CALIFORNIA



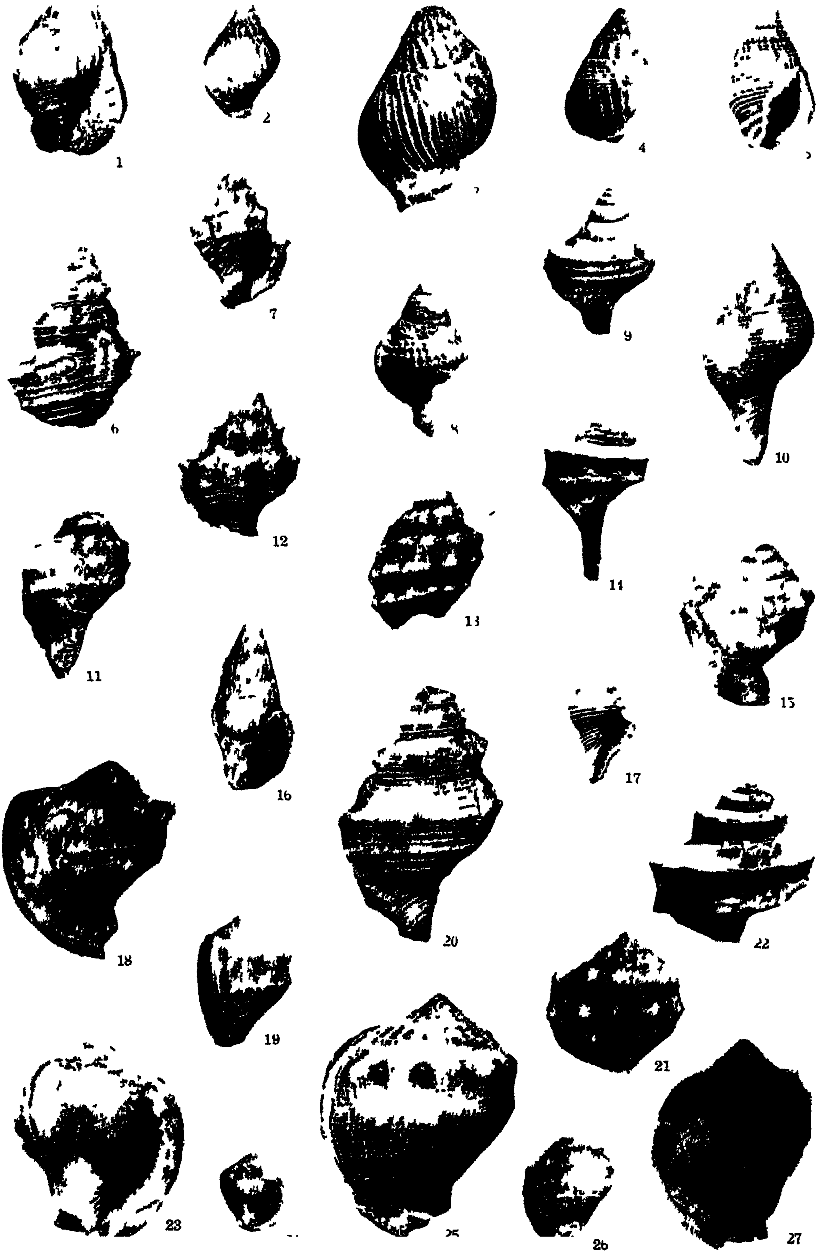
VOKES: EOCENE MOLLUSCA OF CALIFORNIA

PLATE 18

FIGURE 1. *Conus caleocius* n. sp. × 2.5; Hypotype 15786, loc. A-1165.
FIGURE 2. *Conus hornii umpquaensis* Turner × 2; Hypotype 15783, loc. A-975.
FIGURE 3. *Conus hornii umpquaensis* Turner × 2; Hypotype 15784, loc. A-1164.
FIGURE 4. *Bonellitia (?) megapex* n. sp. × 3.5; Paratype 15890, loc. 672.
FIGURE 5. *Bonellitia (?) megapex* n. sp. × 3.5; Holotype 15889, loc. 672.
FIGURE 6. *Ancilla (Spirancilla) gabbi* (Cossmann). × 2; Hypotype 15787, loc. 672.
FIGURE 7. *Conus caleocius* n. sp. × 2.5; Holotype 15785, loc. 3310.
FIGURE 8. *Coralliophila dubia* (Merriam & Turner). × 1; Topotype 15801, loc. A-1314.
FIGURE 9. *Coralliophila dubia* (Merriam & Turner). × 1; Topotype 15801, loc. A-1314.
FIGURE 10. *Ancilla (Spirancilla) gabbi* (Cossmann). × 2; Hypotype 15788, loc. 672.
FIGURE 11. *Falsifusus marysvillensis* (Merriam & Turner). × 1.5; Hypotype 15791, loc. 1817.
FIGURE 12. *Marginella (Leptegouana ?) hulini* n. sp. × 3.5; Paratype 15893, loc. A-1014.
FIGURE 13. *Marginella (Leptegouana ?) hulini* n. sp. × 3.5; Holotype 15891, loc. A-1016.
FIGURE 14. *Marginella (Leptegouana ?) hulini* n. sp. × 3.5; Paratype 15892, loc. A-1016.
FIGURE 15. *Fusinus ucalius* n. sp. × 1.3; Holotype 15477, loc. A-816.
FIGURE 16. *Umpquaia flangella* n. sp. × 1.2; Holotype 15793, loc. A-1020.
FIGURE 17. *Umpquaia flangella* n. sp. × 1.2; Paratype 15794, loc. A-1154.
FIGURE 18. *Voluta (?) eomagna* n. sp. × 1; Holotype 15789, loc. A-973.
FIGURE 19. *Uromitra (?) cretacea* (Gabb). × 2; Hypotype 15894, loc. A-1164.
FIGURE 20. *Umpquaia flangella* n. sp. × 1; Holotype 15793, loc. A-1020.
FIGURE 21. *Umpquaia flangella* n. sp. × 1; Paratype 15795, loc. A-1154.
FIGURE 22. *Lyria andersoni* Waring. × 1; Hypotype 15790, loc. 3958.
FIGURE 23. *Pseudoliva lineata* Gabb. × 1; Hypotype 15796, loc. 4169.
FIGURE 24. *Lyria andersoni* Waring. × 1; Hypotype 15790, loc. 3958.
FIGURE 25. *Janiopsis (?) kreyenhageni* (Arnold). × 3; Topotype 15897, loc. 7155.
FIGURE 26. *Harpa (Eocithara) clarki* Vokes. × 1.4; Holotype 15792, loc. A-1165.
FIGURE 27. *Janiopsis (?) kreyenhageni* (Arnold). × 2; Topotype 15896, loc. 7155.
FIGURE 28. *Janiopsis (?) kreyenhageni* (Arnold). × 2; Topotype 15895, loc. 7155.
FIGURE 29. *Janiopsis (?) kreyenhageni* (Arnold). × 2; Topotype 15898, loc. 7155.
FIGURE 30. *Umpquaia oregonensis* Turner. × 1; Holotype 33202, loc. A-662.

PLATE 19

FIGURE 1. *Molopophorus antiquatus* (Gabb). × 2.1; Hypotype 15940, loc. A-818.
FIGURE 2. *Molopophorus antiquatus* (Gabb). × 2.1, Hypotype 15939, loc. A-819.
FIGURE 3. *Molopophorus antiquatus* (Gabb). × 2.1; Hypotype 15938, loc. A-819.
FIGURE 4. *Molopophorus cretaceus* (Gabb). × 2; Hypotype 15937, loc. A-1366.
FIGURE 5. *Molopophorus aequicostatus* n. sp. × 2; Holotype 15941, loc. 672.
FIGURE 6. *Ranella domenginica* n. sp. × 1; Syntype 15804, loc. 672.
FIGURE 7. *Muricopsis (?) whitneyi* var. × 1.5; Hypotype 15797, loc. A-1020.
FIGURE 8. *Cymatium (Lampusia)* n. sp. × 1.5; figured specimen 15802, loc. 672.
FIGURE 9. *Pseudoperissolax blakei* (Conrad). × 2.5; Hypotype 15840, loc. 7200. Nucleus.
FIGURE 10. *Ranellina pilsbryi* Stewart. × 1.5; Hypotype 15805, loc. 672.
FIGURE 11. *Ficopsis meganosensis packardi* Merriam & Turner. × 1.5; Hypotype 15813, loc. 1817.
FIGURE 12. *Muricopsis (?) whitneyi* n. var. × 1.5; Hypotype 15798, loc. A-1020.
FIGURE 13. *Ficopsis meganosensis packardi* Merriam & Turner. × 1.5; Hypotype 15814, loc. 1817.
FIGURE 14. *Pseudoperissolax blakei praeblakei* n. subsp. × 1; Paratype 15800, loc. 1817.
FIGURE 15. *Galeodea sutterensis* Dickerson. × 1; Hypotype 15812, loc. 1817.
FIGURE 16. *Cumia harrisi* (Dickerson). × 2; Topotype 15899, loc. 1817.
FIGURE 17. *Ranellina pilsbryi* Stewart. × 1.5; Hypotype 15806, loc. 672.
FIGURE 18. *Galeodea sutterensis meganosensis* n. subsp. × 1; Holotype 31244, loc. 3152.
FIGURE 19. *Galeodea tuberculiformis* Hanna. × 1.2; Hypotype 15809, loc. 672. Specimen with only two nodose carinae.
FIGURE 20. *Ranella domenginica* n. sp. × 1; Syntype 15803, loc. 672.
FIGURE 21. *Galeodea tuberculiformis* Hanna. × 1.2; Hypotype 15808, loc. 672. Specimen with three nodose carinae.
FIGURE 22. *Pseudoperissolax blakei praeblakei* n. subsp. × 1; Holotype 15799, loc. 1817.
FIGURE 23. *Galeodea tuberculiformis* Hanna. × 1; Hypotype 15807, loc. 672. Note characteristically denticulate outer lip.
FIGURE 24. *Galeodea tuberculiformis* Hanna. × 1.2; Hypotype 15811, loc. 672. Immature form with nodose carina on shoulder of whorl only.
FIGURE 25. *Galeodea tuberculiformis* Hanna. × 2; Hypotype 11783, loc. 672. Specimen with rudimentary third nodose carina; note the characteristic beaded spiral sculpture.
FIGURE 26. *Galeodea tuberculiformis* Hanna. × 1.2; Hypotype 15810, loc. 672. Position of third carina indicated by a strong spiral thread.
FIGURE 27. *Galeodea tuberculiformis* Hanna. × 1; Hypotype 15807, loc. 672.



VOKES. EOCENE MOLLUSCA OF CALIFORNIA

VOKES EOCENE MOLLUSCA OF CALIFORNIA

PLATE 20

FIGURE 1. *Rimella* (*Macilentos*) *macilenta* White. × 1.8; Hypotype 15819, loc. A-1165. Cast of outer lip of a large specimen

FIGURE 2. *Rimella* (*Macilentos*) *macilenta* White. × 1.8; Topotype 15816, loc. A-1016.

FIGURE 3. *Bittium* (?) *dumblei* (Dickerson). × 2; Topotype 15828, loc. 672

FIGURE 4. *Rimella* (*Macilentos*) *macilenta* White. × 1.8; Hypotype 15817, loc. A-976.

FIGURE 5. *Rimella* (*Macilentos*) *macilenta* White. × 1.8; Hypotype 15818, loc. A-1165

FIGURE 6. *Rimella* (*Macilentos*) *macilenta oregonensis* Hendon. × 1; Holotype = Turner (1938) *pl. 18, f. 3.*

FIGURE 7. *Terebellum californicum* n. sp. × 1.5; Hypotype 15822, loc. 3296.

FIGURE 8. *Terebellum californicum* n. sp. × 1.3; Holotype 15820, loc. A-976.

FIGURE 9. *Eocypraea castacensis* (Stewart). × 1.1; Hypotype 33808, loc. 3296.

FIGURE 10. *Rimella* (*Macilentos*) *macilenta oregonensis* Hendon. × 1; Paratype = Turner (1938) *pl. 18, f. 1.*

FIGURE 11. *Terebellum californicum* n. sp. × 1.3; Paratype 15821, loc. A-1164.

FIGURE 12. *Keilostoma californicus* n sp. × 2; Holotype 15833, loc. A-819

FIGURE 13. *Keilostoma californicus* n. sp. × 2; Paratype 15834, loc. A-976.

FIGURE 14. *Eocypraea castacensis* (Stewart). × 1; Hypotype 15815, loc. A-1282.

FIGURE 15. *Loxotrema turrita* Gabb. × 1; Hypotype 15832, loc. A-1020.

FIGURE 16. *Loxotrema turrita* Gabb. × 1; Topotype 15830, loc. A-1154.

FIGURE 17. *Loxotrema turrita* Gabb. × 1; Topotype 15829, loc. A-1154.

FIGURE 18. *Loxotrema turrita* Gabb. × 2; Topotype 15831, loc. A-1154

FIGURE 19. *Loxotrema turrita* Gabb. × 1; Hypotype 15832, loc. A-1020.

FIGURE 20. *Spiroglyphus* (?) *tejonensis* Arnold. × 1; Hypotype 15836, loc. 7154.

FIGURE 21. *Spiroglyphus* (?) *tejonensis* Arnold. × 1; Hypotype 15835, loc. 7154.

FIGURE 22. *Spiroglyphus* (?) *tejonensis* Arnold. × 1; Hypotype 15837, loc. 7154.

FIGURE 23. *Potamides carbonicola* Cooper. × 1.5; Topotype 15827, loc. A-1223.

FIGURE 24. *Potamides carbonicola* Cooper. × 1.5; Hypotype 15825, loc A-1020.

FIGURE 25. *Potamides carbonicola* Cooper. × 1.5; Hypotype 15826, loc. A-1020.

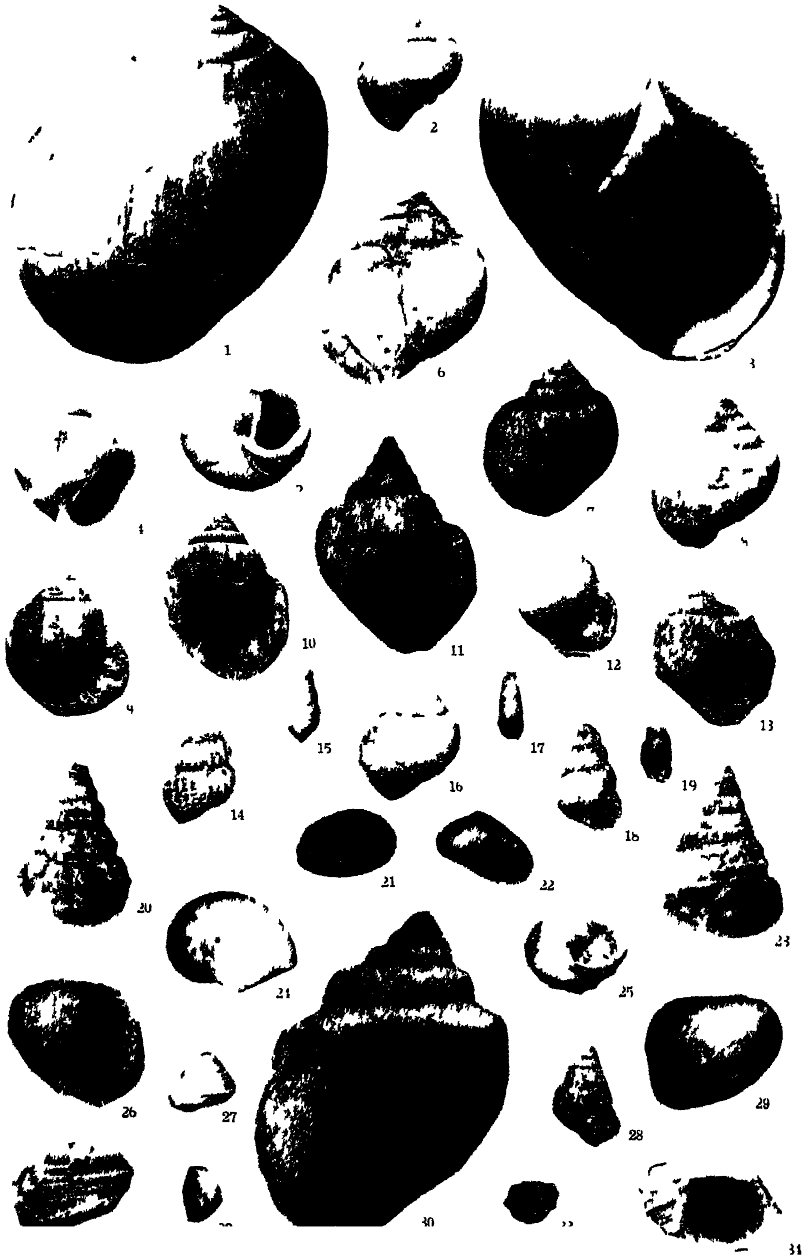
FIGURE 26. *Potamides carbonicola* Cooper. × 1.5; Hypotype 15824, loc. A-1020.

FIGURE 27. *Potamides carbonicola* Cooper. × 1.5; Topotype 15823, loc. 7155.

PLATE 21

FIGURE 1. *Tectarius ligniticus* n. sp. × 1.5; Holotype 15838, loc. 7005.
FIGURE 2. *Polinices gesteri* (Dickerson). × 3.5; Hypotype 15846, loc. 672.
FIGURE 3. *Tectarius ligniticus* n. sp. × 2; Hypotype 15839, loc. 7155.
FIGURE 4. *Tectarius ligniticus* n. sp. × 1.5; Holotype 15838, loc. 7005.
FIGURE 5. *Natica domenginica* n. sp. × 3; Paratype 15844, loc. 672.
FIGURE 6. *Polinices gesteri* (Dickerson). × 3.5; Hypotype 15845, loc. 672.
FIGURE 7. *Xenophora* n. sp. × 2; figured specimen 15842, loc. A-1165.
FIGURE 8. *Natica domenginica* n. sp. × 3; Holotype 15843, loc. 672.
FIGURE 9. *Neverita globosa* Gabb. × 1.5; Hypotype 15854, loc. 7155.
FIGURE 10. *Crepidula (Spirocrypta) inornata* Dickerson. × 2.5; Holotype 11804, loc. 672.
FIGURE 11. *Crepidula (Spirocrypta) inornata* Dickerson. × 3.5; Topotype 15841, loc. 672.
FIGURE 12. *Polinices (Euspira) nuciformis* (Gabb). × 1.3; Hypotype 15847, loc. A-1016.
FIGURE 13. *Polinices (Euspira) nuciformis* (Gabb). × 1.5; Hypotype 15849, loc. A-1165.
FIGURE 14. *Polinices (Euspira) nuciformis* (Gabb) × 1.4; Hypotype 15848, loc. A-1165
FIGURE 15. *Neverita globosa* Gabb. × 1.5; Hypotype 15850, loc A-1020
FIGURE 16. *Neverita globosa* Gabb. × 1.5; Hypotype 15852, loc. A-1020.
FIGURE 17. *Neverita globosa* Gabb. × 1.5; Hypotype 15851, loc. A-1020.
FIGURE 18. *Neverita globosa* Gabb. × 1.5; Hypotype 15853, loc. A-1020.
FIGURE 19. *Neverita globosa* Gabb. × 1.5; Hypotype 15850, loc. A-1020.
FIGURE 20. *Ampullella schencki* n. sp. × 1.5; Paratype 15857, loc. 4170.
FIGURE 21. *Ampullella schencki* n. sp. × 1.5; Paratype 15858, loc. 4170.
FIGURE 22. *Crommium andersoni* (Dickerson). × 1.5; Hypotype 15860 loc. A-1154.
FIGURE 23 *Crommium andersoni* (Dickerson). × 1.5; Hypotype 15859, loc. A-1154
FIGURE 24. *Neverita globosa reefensis* n. subsp. × 1.5; Holotype 15855, loc. A-819.
FIGURE 25. *Neverita globosa reefensis* n. subsp. × 1.3; Holotype 15855, loc. A-819.
FIGURE 26. *Ampullella schencki* n. sp. × 1.5; Holotype 15856, loc. 4170.

VOKES EOCENE MOLLUSCA OF CALIFORNIA



VOKES EOCENE MOLLUSCA OF CALIFORNIA

PLATE 22

FIGURE 1 *Cernina* (*Eocernina*) *hannibali* (Dickerson). × 1; Hypotype 15861, loc. 3296.

FIGURE 2 *Amaurellina* (?) *multiangulata* n. sp. × 1.3; Paratype 15868, loc. A-1016.

FIGURE 3 *Cernina* (*Eocernina*) *hannibali* (Dickerson). × 1; Hypotype 15861, loc. 3296.

FIGURE 4 *Amaurellina caleocia* n. sp. × 1.5; Holotype 33781, loc. 672

FIGURE 5 *Amaurellina caleocia* n. sp. × 1.5; Holotype 33781, loc. 672.

FIGURE 6 *Amaurellina caleocia* n. sp. × 1.5; Paratype 15862, loc. 672

FIGURE 7 *Amaurellina hendoni* Turner. × 1; Holotype = Turner (1938) *pl. 20, f. 11*.

FIGURE 8 *Amaurellina* (?) *multiangulata* n. sp. × 1.3; Holotype 15866, loc. A-1016.

FIGURE 9 *Amaurellina garzaensis* n. sp. × 2; Paratype 15864, loc. A-1164.

FIGURE 10 *Amaurellina hendoni* Turner. × 1; Paratype 33178, loc A-662

FIGURE 11. *Pachycrommium* (?) *clarki* (Stewart). × 1; Hypotype 15870, loc A-1012.

FIGURE 12 *Amaurellina garzaensis* n. sp × 2; Paratype 15865, loc. A-1164.

FIGURE 13 *Amaurellina* (?) *multiangulata* n. sp. × 1.3; Paratype 15867, loc. A-1016.

FIGURE 14. *Acrilla* (*Ferminoscala*) *tejonensis* (Dickerson). × 2; Topotype 15882, loc. 672.

FIGURE 15. *Odostomia griswoldensis* n. sp. × 3.5; Holotype 15887, loc. A-1154.

FIGURE 16. *Amaurellina garzaensis* n. sp. × 2; Holotype 15863, loc.A-1164.

FIGURE 17. *Melanella coalingana* n. sp. × 3.5; Holotype 15873, loc. 1817

FIGURE 18. *Acrilla* (*Ferminoscala*) *tejonensis* (Dickerson). × 2; Topotype 15881, loc 672.

FIGURE 19. *Odostomia griswoldensis* n. sp. × 3.5; Paratype 15888, loc. A-1154.

FIGURE 20. *Calliovarica eocensis* n. sp. × 1.5; Paratype 15885, loc. 1817

FIGURE 21. *Homalopoma wattsi* (Dickerson). × 2; Hypotype 15871, loc. 1817.

FIGURE 22. *Homalopoma wattsi* (Dickerson) × 2; Hypotype 15871, loc. 1817.

FIGURE 23 *Calliovarica eocensis* n. sp. × 1.5; Holotype 15884, loc. 1817.

FIGURE 24. *Nerita* (*Amphinerita*) *eorex* n. sp. × 2; Paratype 15880, loc A-1281.

FIGURE 25. *Calliovarica eocensis* n. sp. × 1; Holotype 15884, loc 1817.

FIGURE 26 *Nerita* (*Amphinerita*) *eorex* n. sp. × 2; Holotype 15874, loc. A-1165.

FIGURE 27. *Homalopoma umpquaensis domenginensis* n subsp × 2; Holotype 15872, loc 672.

FIGURE 28. *Calliovarica eocensis* n sp. × 1.5; Paratype 15886, loc. 1817.

FIGURE 29. *Nerita* (*Amphinerita*) *eorex* n. sp. × 2; Holotype 15874, loc. A-1165.

FIGURE 30. *Pachycrommium* (?) *clarki* (Stewart). × 1; Hyoptype 15869, loc. A-1016

FIGURE 31. *Nerita* (*Theliostyla*) *triangulata* Gabb. × 2; Hypotype 15875, loc. 7155.

FIGURE 32. *Acmaea* n. sp. × 2.7; figured specimen 15883, loc. A-1164.

FIGURE 33. *Nerita* (*Theliostyla*) *triangulata* Gabb. × 1.5; Hypotype 15876, loc 7155.

FIGURE 34. *Nerita* (*Theliostyla*) *triangulata* Gabb. × 2; Hypotype 15875, loc. 7155.

INDEX*

* To genera, subgenera, sections, species, subspecies, and varieties only.